

UNIVERSIDADE FEDERAL DO PARANÁ

FELIPE SKÓRA NETO

OBRAS DE INFRAESTRUTURA HIDROLÓGICA E INVASÕES DE PEIXES DE  
ÁGUA DOCE NA REGIÃO NEOTROPICAL: IMPLICAÇÕES PARA  
HOMOGENEIZAÇÃO BIÓTICA E HIPÓTESE DE NATURALIZAÇÃO DE  
DARWIN

CURITIBA

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DARWIN

Dissertação apresentada como requisito parcial à obtenção do grau de Mestre em Ecologia e Conservação, no Curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná.

Orientador: Jean Ricardo Simões Vitule

Co-orientador: Vinícius Abilhoa

CURITIBA

2013

Dedico este trabalho a todas as pessoas que foram meu suporte, meu refúgio e minha fortaleza ao longo dos períodos da minha vida.

Aos meus pais Eugênio e Nilte, por sempre acreditarem no meu sonho de ser cientista e me darem total apoio para seguir uma carreira que poucas pessoas desejam trilhar. Além de todo o suporte intelectual e espiritual e financeiro para chegar até aqui, caminhando pelas próprias pernas.

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‘Nós somos aquilo que  
fazemos repetidamente.  
Excelência, então, não é um  
modo de agir, mas um  
hábito. ’

Aristóteles

## RESUMO

Atualmente, os peixes de água doce são considerados uma das faunas mais ameaçadas ao redor do mundo, devido à água doce ser amplamente explorada e impactada pelo homem. Utilizamos água para consumo e produção de alimentos, saneamento, recreação, transporte e produção de energia. Para atender estes usos, utilizamos obras de infraestrutura, como usinas para prover energia elétrica, transposições e diques para controlar o regime de água e seu fluxo para manter a disponibilidade deste recurso aonde há demanda. Apesar dos ecossistemas aquáticos já terem um longo histórico de impactos associado ao uso humano, à taxa de alterações e modificações nunca foi tão alta e exacerbada, sendo um reflexo do domínio humano sobre o planeta.

Uma consequência deste domínio, recentemente trazida à tona é o aumento da similaridade composicional das biotas entre áreas geográficas ao longo do tempo, processo denominado homogeneização biótica. O processo é dinâmico passando diversas vezes por homogeneização, ou o aumento da similaridade das biotas entre as áreas. Mas também passando por processos de diferenciação, aonde a similaridade das biotas entre as áreas diminui. Sendo que o resultado final esperado em escala espaço-temporal ampla seja o de homogeneização, por que um pequeno grupo de espécies se distribuiria por todo o globo aumentando a similaridade total. A homogeneização biótica é dividida em três linhas: Taxonômica, onde se mensura a amplificação da similaridade entre duas ou mais áreas pela identidade taxonômica. Funcional: quando avaliamos amplificações nas similaridades das características ecológicas das espécies como, por exemplo, tamanho, dieta, reprodução, ciclagem de nutrientes. Genética: mede-se a variabilidade do pool genético entre populações das mesmas espécies ou de taxa relacionados, por exemplo, espécies dentro de um mesmo gênero.

A variação da similaridade entre biotas está ligada aos seguintes processos: (I) Introdução de espécies não nativas: Inserção de espécies pode aumentar a similaridade, caso a mesma espécie seja introduzida em múltiplas localidades. Por que ao comparar a similaridade entre estas áreas, está espécie que foi introduzida em comum aumentará a similaridade. Introduções também podem diminuir a similaridade quando espécies distintas são introduzidas em diferentes localidades. É comum, que o efeito de diminuição da similaridade seja verificado logo que uma espécie é introduzida, mas assim que ela se expande pela área, começamos a observar o aumento desta similaridade entre localidades, devido a isto homogeneização deve levar em conta o aspecto temporal. (II) Extirpação de espécies nativas: Aumentamos a similaridade ao retirar espécies que possuam distribuição restrita, presente em poucas localidades ou somente em uma. Por que na comparação entre as áreas, houve a perda da espécie que era diferente nas combinações possíveis. Diminuir a similaridade ocorre caso uma espécie amplamente distribuída seja extirpada. A dinâmica de homogeneização por extirpação é difícil de prever, uma vez que registros são raras e muitas espécies que são consideradas extirpadas podem ser também raras em amostragens. (III) Modificação de habitat: A alteração de habitat atua como um catalisador para os dois fatores anteriores podendo ser de forma sinérgica ou não. Ao alterar um ambiente,

perturba-se a biota local facilitando a introdução de espécies não nativas tanto pela alteração do habitat, quanto pelo distúrbio que ocorre da biota nativa. Dependendo da intensidade do distúrbio podemos ter a extirpação de espécies nativas, por má adaptação ou por competição com espécies introduzidas. Ressalto que não é somente o homem que causa modificações no habitat, mas muitas espécies introduzidas também podem atuar como modificadoras do ambiente, ou facilitadores de outras invasões e extinções.

No 1º capítulo exploro, com uma revisão enviesada, como obras de engenharia hidráulica causam modificações ambientais que podem gerar homogeneização biótica, e proponho o uso de inventários museu, listas de espécies dos relatórios técnicos e trabalhos acadêmicos com lista de espécies para avaliar este processo de maneira temporal. Em geral, obras como represas, usinas, canais e transposições alteram principalmente a conectividade do ambiente aquático, amplificando ou restringindo-a. O aumento da conectividade de forma geral permite um trânsito maior de espécies entre regiões, tornando as biotas das regiões mais similares. A quebra de conectividade pode isolar áreas e populações acarretando diminuição da similaridade devido ao obstáculo para migração. Mas como a diminuição de conectividade está associada a represamentos, a homogeneização acontecerá devido à introdução de das mesmas espécies não nativas nas áreas alteradas. Através da ampliação do estudo da homogeneização biótica, podemos resgatar os dados gerados por estas obras mesmo que sejam necessárias adaptações, para que ajudem a avaliar a extensão do impacto humano na diversidade entre áreas (diversidade beta), em relação à introdução e extirpação de espécies e alterações do habitat de maneira temporal. Auxiliando a elucidar dinâmicos e potenciais padrões na variação da diversidade espaço-temporal em vários níveis de organizações biológicas. Definindo de forma mais clara e eficaz o papel relativo de cada um destes fatores para homogeneização biótica.

O capítulo 2 é um estudo de caso que mostra como podemos resgatar dados de inventários para quantificar a homogeneização relacionada a uma obra de engenharia hidráulica. Quantificamos através de dados de relatórios e trabalhos acadêmicos a tendência de homogeneização/diferenciação biótica da ictiofauna após a construção de Itaipu e o aumento de conectividade gerado pela quebra de um filtro biogeográfico entre duas ecoregiões distintas: Alto Paraná e Baixo Paraná. A construção de Itaipu inundou as Sete Quedas, uma série de quedas d'água que atuava como um filtro ecológico para ictiofaunas das ecoregiões mencionadas. Além da introdução via inundação das Sete quedas, outros mecanismos de introdução de espécies como: pesca esportiva, aquicultura e aquariofilia também foram avaliados. Homogeneização biótica, taxonômica e funcional, foi analisada comparando os subgrupos das ecoregiões antes da construção e no tempo presente. Para quantificar o processo, foram utilizados os índices de similaridade de Jaccard, Bray-Curtis, diversidade beta de Whittaker e o método gráfico 'NMDS'. A homogeneização biótica ocorreu principalmente em função do movimento das espécies da ecoregião do Baixo Paraná para o Alto Paraná. O índice Jaccard mostrou um aumento de ~10% na similaridade taxonômica entre as ictiofaunas das ecoregiões considerando todo mecanismo de invasão, e de ~7% considerando somente as invasões decorrentes da usina. Houve homogeneização funcional em relação ao tamanho corporal, a fauna do Alto Paraná aumentou em seu

tamanho médio devido principalmente a ascensão de grandes Siluriformes. Este processo de homogeneização foi um impacto imprevisto da construção da usina, que de maneira simples pode ser avaliado pelo resgate de dados de lista de espécies e de métricas simples.

O 3º Capítulo é um desdobramento do capítulo anterior, considerando a diferente taxa de sucesso de invasão e estabelecimento de diversas espécies da ictiofauna do Baixo Paraná para o Alto Paraná. Avalio se a hipótese de naturalização de Darwin explicaria as diferentes taxas de sucesso de estabelecimento encontradas. Darwin no livro origem das espécies propõe a que espécies sendo introduzidas em áreas onde apresentam taxa relacionados sofreriam mais competição e teriam menor sucesso para se estabelecer. Utilizando a base de dados anteriores somente com as espécies nativas do baixo, como potenciais colonizadores da região do Alto Paraná. Verificamos através de três métodos a hipótese de naturalização de Darwin. Primeiramente foi avaliado se a presença de congêneros afetou ou não o sucesso de estabelecimento através de uma tabela de contingência utilizando o teste exato de Fisher, com as contagens em nível de gênero. As espécies com potencial de colonizar foram divididas em subgrupos de sucesso e fracasso pela presença ou ausência de congêneros nativos. Numa segunda forma de abordagem, utilizamos as características ecológicas das espécies e suas relações de distância para quantificar o nicho, assumindo que quando maior a similaridade das características maior a competição. Desta relações foi tirada duas métricas. Similaridade do invasor para a nativa mais próxima (DNNS) e Média das similaridades de toda a comunidade nativa para o Invasor (MDNS). As características foram transformadas em uma matriz de similaridade através da métrica de Gower, e os subgrupos (sucesso e fracasso) comparados através do teste U de Mann-Whitney. O terceiro método é um modelo conceitual, considerando a matriz das características funcionais do método anterior, obtemos o valor de similaridade de cada invasora para cada uma das espécies nativas. Este *pool* de valores para cada invasora é ajustado a um modelo (I) Exponencial: A maioria das espécies nativas tem pouca similaridade com a invasora. (II) Logarítmico: Existem muitas espécies nativas similares à invasora. (III) Linear: Existem espécies similares e dissimilares em proporções parecidas, que não se encaixam nos modelos anteriores. Para todos os modelos os padrões de similaridade têm implicações sobre competição e adequabilidade de recursos. De forma simplificada, poderíamos atribuir o sucesso e fracasso à ausência/presença de competição ou adequabilidade/falta de adequabilidade de habitat. Após o ajuste, o melhor modelo é selecionado pelo critério de informação de Akaike. As frequências entre os grupos sucesso e fracasso é comparada por um teste de  $\chi^2$ . O resultado geral do teste de Fisher mostrou que não existe relação entre o sucesso e a presença ou não de congêneros, nem mesmo entre as ordens monofiléticas, como Siluriformes e Characiformes. As métricas de distância não foram significativas: MDNS ( $p = 0.52$ ) e DNNS ( $W = 5637$ ,  $p = 0.27$ ), mas há uma tendência das espécies que tiveram sucesso serem mais diferentes das nativas mais próximas. Todos os ajustes propostos pelo modelo conceitual foram possíveis, mas não apresentaram frequências diferentes entre os grupos de sucesso e fracasso ( $\chi^2 = 4.204$ , d.f. = 2,  $p > 0.12$ ). Apesar da impossibilidade em corroborar a hipótese devida possivelmente a fatores como escala espacial ampla e incapacidade de identificar mecanismos neutros. As



tendências mostradas nas métricas de similaridade, com um refinamento espacial onde a competição for mais realista de ocorrer podem e devem ser testadas futuramente. Este trabalho é um avanço em relação aos métodos e abordagens usados, além disso, tivemos um fator poderoso em nossa análise em relação a todos os demais artigos que testaram tal hipótese até o momento: utilizamos um *pool* de espécies invasoras realísticas ao invés de estimar sucesso e fracassos utilizando espécies de várias regiões do mundo, o que é um viés muito maior.

A homogeneização biótica é um problema que veio a tona recentemente, mas que pode ser abordada de forma eficiente para ambientes de água doce, através do resgate de lista de espécies, relatórios técnicos e trabalhos acadêmicos de autoecologia, valorizando-os e mostrando que devem ser bem feitos para gerar ciência. Com pequenos ajustes nos dados e através de métricas simples podemos quantificar de forma temporal mudanças na similaridade composicional da biota entre regiões após alterações do habitat por obras de engenharia hidráulica. Como exemplo o estudo de caso onde uma obra foi responsável por 7 dos 10% de incremento da similaridade taxonômica, devido a aumentar a conectividade entre as regiões. O que ressalta a importância de avaliar os locais e a fauna antes da instalação destas estruturas. Por que a biota definitivamente irá mudar, e esta mudança pode ser quantificada e utilizada para testar teorias na área de invasões biológicas. Com estes mesmo dados e séries obtidas podemos tentar elucidar padrões de invasão como a hipótese de naturalização, que neste caso mostrou uma tendência à invasão das espécies distintas da comunidade nativa.

Palavras-chave: Homogeneização biótica, invasão biológicas, Naturalização de Darwin, Engenharia hidráulica, crise da biodiversidade

## ABSTRACT

Freshwater fish are among the most endangered fauna worldwide because they have high endemism rates and have been subjected to a long history of human-induced impacts. Human-caused environmental modifications by hydraulic engineering have accelerated the biodiversity impoverishment crises. Local and endemic species are being replaced by widespread exotic ones that lead to a global homogenization of biotas.

Chapter 1: Explore and highlight the biotic homogenization concept and metrics as a tool to quantify, monitor and deal with these human-caused environmental modifications. Biotic homogenization quantifies biotic similarity over time and space, and it is achieved using freshwater fish species lists to measure and monitor the species turnover between areas. Lists and inventories are essential and the homogenization concept can be more used to ascertain the nature and extent of human impacts on biodiversity dynamics over time, for example in relation to the relative importance of major drivers in the process: habitat alteration and species introductions. Biotic homogenization studies are even more relevant in developing mega-diverse regions of the world, where habitats and assemblages have been severely and rapidly changed without proper studies. Conservation professionals should regard engineering feats as primary drivers of biotic homogenization that can be quantified and monitored with few data adjustments from inventories and with simple similarity metrics to plan fish conservation especially in megadiverse regions like: Neotropical, Ethiopian and Oriental realms, where it is still a new research field.

Chapter 2: We quantify biotic homogenization of fish fauna caused by the elimination of a natural barrier between two freshwater ecoregions. We also evaluated fish introductions by different mechanisms such as aquaculture, angling and the aquarium trade in the homogenization of fish assemblages. The relative importance of native extinctions in the homogenization process was assessed by simulating the exclusion of threatened species in the data set. A fish species list of the Parana River Basin was organized in a subset of species distributions, according to pre- and post-introductions caused by the elimination of the natural barrier and by other mechanisms. Biotic homogenization was verified by the use of Jaccard's and Bray–Curtis's coefficients, Whittaker's beta diversity index, non-metric multidimensional scaling analysis (NMDS) and nonparametric tests. For all subsets of species distributions, we observed an increase in the number of non-native species in common related to the introductions. Between 40 and 52% of the species currently present in the Upper Parana Basin dispersed upstream from the Lower Parana after the construction of Itaipu Dam, including at least 1 class, 2 orders, 4 families and 16 genera of fish. Jaccard's coefficient between the Upper and Lower Parana River increased by 6–7.5% only considering the Itaipu Dam influence and 10.5% considering all mechanisms of fish introductions. More than 50% of the increase in similarity was caused by the elimination of the barrier. Our results indicated functional homogenization related to large-bodied Siluriformes (catfish). Itaipu Lake flooded a natural barrier and allowed hydrologic connectivity between the Upper and Lower Parana River, and many fishes of the lower part of the river were able to colonize the upper stretches. The homogenization of the two assemblages between these adjacent aquatic regions was an unpredicted result of hydropower implementation. Introductions by dam can also shift longitudinal and latitudinal body size patterns (i.e. Bergmann's rule).

Chapter 3: While being able to understand and predict invasion success had been a long term goal of biological invasions studies. Experimental approaches are needed to validate some proposed theories concerning establishment success. Using data from a quasi-natural experiment where the elimination of a vicariant barrier for fishes mixed two distinct faunas, especially allowing a massive unidirectional fish invasion, to happen on downstream-upstream direction. We investigate this regional scale fact under the optic of Darwin's naturalization hypothesis. Invading species would have reduced chance to establish if a taxonomic/functional related native were present recipient area. The major advance this study provides is reducing the 2 major sources of errors of previous studies using freshwater fish fauna. We know realistically the potential invader donor pool, and use functional traits to quantify niche use, as taxonomy may not reflect competition. Relatedness between the species pools were done through taxonomy and measure of 'alpha niche', the latter utilizing species most common functional traits available. The 'alpha niche' measures were also used through a conceptual model, the 'alpha niche' of an invader was compared one by one with the entire native community, to see how much of native community was similar to that invader. Conceptual models and taxonomical contingences tests shows no support for Darwin's hypothesis. However, considering the large scale analyzed. The order Characiformes showed on taxonomic testing, a signal that with some caution could be interpreted as confirmation. A high failure count of species with native congeners present, this demands further investigation. 'Alpha niche' metrics shows that distance from invader to the native species most functional similar agrees with Darwin's hypothesis, successful invaders were more dissimilar to native fauna than failed ones. Increasing our ability to measure traits related to competition and reducing scale to where biotic interactions matters, might reveal that the methodologies considering nearest species and the conceptual model to be effective predictors of invasion success. Biotic homogenization is a recent problem that can be effectively measured on freshwater ecosystems through the rescue of technical reports, museum inventories and academic studies. Doing so valorize the effort on constructing good reports and autoecology works. These data with minor adjustments e simple similarity metrics can be used to quantify temporal changes in biotic similarity between areas altered by hydraulic structures. This has been done on chapter 2, where we show that a dam increased similarity 10% an unexpected impacts. This case study shows how we can set in motion studies through the rescue of those species list and the importance to evaluate where we are building those structures. The same data can also be used to test theories on other fields, as biological invasions. Darwin's naturalization hypothesis show a tendency that invaders species on that are were less similar to native species than species that failed to establish. This was achieved with data mining from above mentioned reports concerning species characteristics. This reveals how integrative a single field and tool can be to integrate impact assessing, identification of biotic drivers that leads to fish fauna impoverishment.

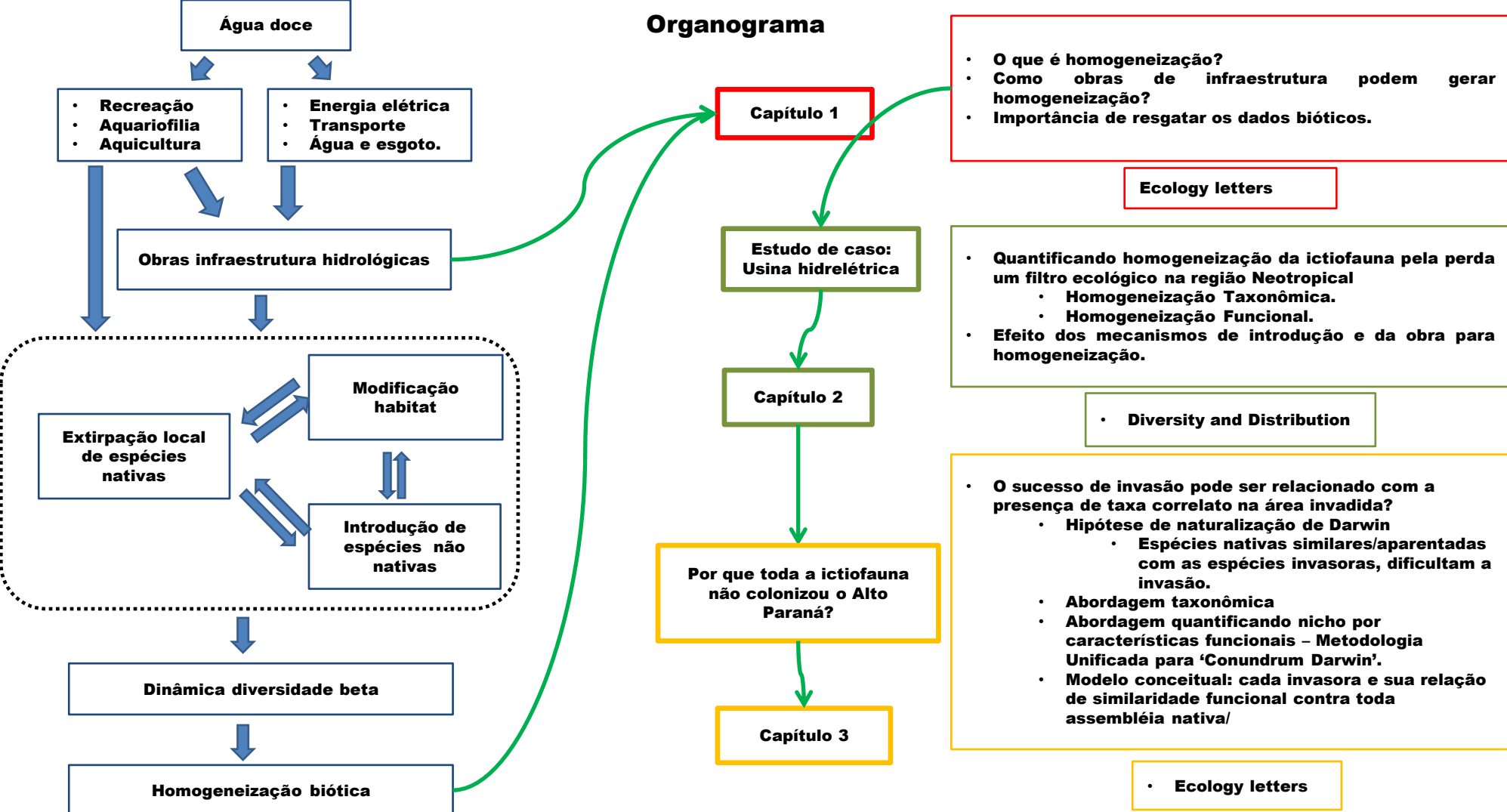
Key words: Biotic homogenization, Biological Invasion, Darwin's Naturalization, Dams, Biodiversity crisis.

## SUMÁRIO

<b>ORGANOGRAMA DA DISSERTAÇÃO.....</b>	<b>14</b>
<b>1. CAPÍTULO 1: Homogenization framework a new tool for understanding threat of infrastructure engineering to freshwater fishes in megadiverse countries. ....</b>	<b>15</b>
<b>1.1. Abstract.....</b>	<b>16</b>
<b>1.2. Introduction.....</b>	<b>17</b>
<b>1.3. The importance of homogenization framework .....</b>	<b>21</b>
<b>1.4. Dams and fish passage.....</b>	<b>24</b>
<b>1.5. Transposition.....</b>	<b>27</b>
<b>1.6. Conclusion and perspectives.....</b>	<b>30</b>
<b>1.7. References.....</b>	<b>33</b>
<b>2. CAPÍTULO 2: Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. ....</b>	<b>41</b>
<b>2.1. Abstract.....</b>	<b>42</b>
<b>2.2. Introduction.....</b>	<b>42</b>
<b>2.3. Methods.....</b>	<b>43</b>
<b>2.4. Results.....</b>	<b>45</b>
<b>2.5. Discussion.....</b>	<b>47</b>
<b>2.6. References.....</b>	<b>49</b>
<b>3. CAPÍTULO 3: Revisiting Darwin's naturalization conundrum: evaluating a natural experiment of massive freshwater fish invasion on a disrupted filter. ....</b>	<b>52</b>
<b>3.1. Abstract.....</b>	<b>54</b>
<b>3.2. Introduction.....</b>	<b>55</b>
<b>3.3. Material and methods.....</b>	<b>58</b>
<b>3.4. Results.....</b>	<b>63</b>
<b>3.5. Discussion.....</b>	<b>67</b>

<b>3.6. References</b> .....	<b>71</b>
<b>4. Conclusão geral</b> .....	<b>74</b>
<b>5. Apêndices</b> .....	<b>75</b>

# Organograma



**Fluxograma de lógica unificação dos capítulos:** A água é um recurso muito utilizado pelo homem, para recreação, transporte, saneamento, geração de energia. E a necessidade que temos deste recurso vem aumentando ao longo do tempo. Para sanar nossas necessidades, construímos diversos tipos de obras nos corpos de água, que alteram conectividade de rios e seus fatores abióticos e bióticos. Não somente alteramos estes últimos fatores por obras, mas também pelo efeito que nosso esgoto e nossas atividades recreativas. Um grande reflexo do uso dos corpos da água é uma tríade de impactos que são sinérgicos e que modificam a estruturação das comunidades. A mudança que a comunidade sofre devido aos estressores pode ser mensurada comparando similaridades da composição das espécies entre áreas em uma dinâmica temporal. Este procedimento de mensurar diversidade entre áreas, diversidade beta, é o que se ocupa o estudo de homogeneização biótica. Este fenômeno veio a tona recentemente, sobre a preocupação do homem estar transformando rapidamente a distribuição das espécies por sua capacidade de alterar o ambiente e transportar organismos ao redor do globo. Tornando as faunas cada vez mais similares a nível global. O Capítulo 1 busca revisar e trazer a tona para profissionais da construção e da ciências biológicas a importância de considerar obras como potenciais homogeneizadores bióticos. Além de utilizar os dados já obtidos para mensurar este efeito de maneira temporal, melhorando nossa compreensão deste fenômeno pouco explorado em várias regiões do globo. O capítulo 2, é uma aplicação prática do uso de relatórios e dados de inventário para quantificar a homogeneização taxonômica e funcional da ictiofauna causada por uma usina hidrelétrica e outros mecanismos de introdução. O capítulo 3, é uma extensão sobre o motivo de que somente algumas espécies puderam se estabelecer em uma nova região após a construção da usina. Analisamos as diferentes taxas de sucesso sobre a perspectiva da hipótese de naturalização de Darwin. Através de três diferentes metodologias: Taxonômica, ‘nicho alfa’ através de características funcionais, e expandindo o uso destas características propomos um modelo conceitual para analisar a relação de similaridade de cada invasor para cada membro da assembleia nativa.

**CAPÍTULO 1: BIOTIC HOMOGENIZATION: A TOOL TO QUANTIFY AND MONITOR IMPACTS OF INFRASTRUCTURE ENGINEERING TO FRESHWATER FISHES IN MEGADIVERSE COUNTRIES**

**CAPÍTULO 1: HOMOGENEIZAÇÃO BIÓTICA COMO UMA FERRAMENTA PARA QUANTIFICAR E MONITORAR IMPACTOS DE OBRAS DE ENGENHARIA SOBRE PEIXES DULCÍCOLAS EM PAISES MEGADIVERSOS.**

Este capítulo está formatado nas normas do periódico 'Ecology letters', para a seção Ideas and Perspectives.

# **BIOTIC HOMOGENIZATION: A TOOL TO QUANTIFY AND MONITOR IMPACTS OF INFRASTRUCTURE ENGINEERING TO FRESHWATER FISHES IN MEGADIVERSE COUNTRIES**

Felipe Skóra<sup>1,2,3</sup>

Vinícius Abilhoa<sup>2</sup>

Jean Ricardo Simões Vitule<sup>1,2,3</sup>

<sup>1</sup> Laboratório de Ecologia e Conservação, Departamento de Engenharia Ambiental, Setor de Tecnologia, Universidade Federal do Paraná, 81531-970, Curitiba, Paraná, Brasil; <sup>2</sup> Grupo de Pesquisas em Ictiofauna, Museu de História Natural Capão da Imbuia, Prefeitura de Curitiba, Rua Prof. Benedito Conceição, 407, 82810-080, Curitiba, Paraná, Brasil; <sup>3</sup> P.P.G. Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná.

Correspondence:

Jean Ricardo Simões Vitule, Laboratório de Ecologia e Conservação, Departamento de Engenharia Ambiental, Setor de Tecnologia, Universidade Federal do Paraná, 81531-970, Curitiba, Paraná, Brasil.

Telephone: +554133613012

E-mail: biovitule@gmail.com

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## Abstract

Freshwater fish are among the most endangered fauna worldwide because they have high endemism rates and have been subjected to a long history of human-induced impacts. Human-caused environmental modifications by hydraulic engineering have accelerated the biodiversity impoverishment crises. Local and endemic species are being replaced by widespread exotic ones that lead to a global homogenization of biotas. We explore and highlight the biotic homogenization concept and metrics as a tool to quantify, monitor and deal with these human-caused environmental modifications. Biotic homogenization quantifies biotic similarity over time and space, and it is achieved using freshwater fish species lists to measure and monitor the species turnover between areas. List and inventories rescues are essential and homogenization concept can be more used to ascertaining the nature and extent of human impacts on biodiversity dynamics over time, for example in relation to relative importance of major drivers in the process: habitat alteration and species introductions. Biotic homogenization studies are even more relevant in mega diverse of the world, where habitats and assemblages have been severely and rapidly changed without proper studies. Conservation professionals should regard engineering feats as primary drivers of biotic homogenization that can be quantified and monitored with appropriated an best possible data adjustment from inventories and with simple similarity metrics to plan fish conservation especially in megadiverse regions like: Neotropical, Ethiopian and Oriental realms, where it is still a new research field.

Key words: Beta diversity, biodiversity crisis, ecological filter, freshwater fish conservation, river management, habitat modification, water resources.

## Introduction

Freshwater is a fundamental human resource that is used as water supply, navigation, recreation and power generation. Those uses generates impacts which could be traced to Roman times (Copp *et al.* 2005), as river pollution, connectivity enablement/restriction of river networks (damming and water transposition) and species translocation worldwide (Cambray 2003a, b, Walters *et al.* 2003, Moyle and Light 1996a, b, Johnson *et al.* 2008, Parker *et al.* 1999, Ricciardi 2007, Blanchet *et al.* 2010, Vitule *et al.* 2012b). Nowadays, the impacts are being exacerbated due to technological development and human distribution, making human footprint to be perceived as a major threat to freshwater ecosystems and biodiversity (Butchart *et al.* 2010, Vorosmarty *et al.* 2010). Freshwater is a small fraction ( $< 0.0095\%$ ) of the Earth's surface containing enormous biodiversity, its home to almost half of all knows fish species with many unique to restricted areas (Helfman *et al.* 2009). Biodiversity comprises a natural resource that can be converted in economic, scientific and educational values from global to local scale (Ehrlich *et al.* 2012). This conversion play an important role in aquatic conservation especially in Neotropical, Ethiopian and Oriental realms (Braga *et al.* 2012) with high diversity but few studies. Regions that also faces important conservation issues concerning habitat alteration and species introductions, leading to a biotic impoverishment of world biota distinction (Lövei *et al.* 2012, Vitule *et al.* 2012b, Simberloff *et al.* 2013).

Biotic homogenization is a phenomenon of biota impoverishment linked with human footprint on freshwater that received attention on the last decade (McKinney and Lockwood 1999). Biotic homogenization by definition is the process where biota loses their distinctiveness over the time (Olden *et al.* 2004). Biotas distinctions are

measured through changes in beta-diversity, or biota similarity between areas over a given period of time, encompassing two results: homogenization and differentiation. Homogenization occurs when compared areas increase in similarity; differentiation is when areas decrease in similarity. Although the beta diversity concept is controversial and under debate (see Legendre *et al.* 2008, Tuomisto and Ruokolainen 2008), it has important practical applications for the assessment of the spatio-temporal turnover of community composition. Beta diversity metrics help in highlighting processes that lead to richness differences between areas, assisting in evaluating ecosystem functioning, management and conservation (Legendre *et al.* 2008). Ecosystem integrity can be measured by beta diversity, composition similarity between areas, changes in three categories: taxonomic, functional and genetic. Taxonomic refers to beta diversity changes over time, or increase/decrease in taxonomic status similarity of two or more biotas. Functional approach uses species traits or life-history strategies variations over time to evaluate changes in ecological functioning between communities. Genetic concerns gene pool diversity, more applied between populations than between communities (McKinney and Lockwood 1999, Olden and Rooney 2006).

Phenomenon of biotic homogenization is complex and integrates aspects of current global crisis such as the introduction of non-native species, extirpation or extinction of native species, climate change and habitat loss or alteration (Rahel 2002, 2007, Rahel and Olden 2008). Being main drivers of beta diversity patterns are species loss/addition and species replacement (Carvalho *et al.* 2012), because those may be influenced by habitat alteration. Species introduction increases similarity among biotas if the same group of introduced species is introduced into areas with few species in common. For example, the same groups of sport and aquaculture

fishes are frequently introduced in river and reservoirs, increasing similarity (Rahel 2000). Similarity decreases when different groups of introduced species are introduced in different biotas with common species (Marchetti 2001). Extirpation can increase or decrease similarity among areas. If areas lose species that are unique to each one but retaining common ones on both areas, similarity will increase. Whereas losing the common species would result in decrease of similarity. Extirpation is a rare event on widespread species because they could recolonize from nearby sources. Homogenization is the expected outcome from extirpation because it targets rare/endemic small sized populations than widespread ones. Habitat alteration acts as a catalyst for introductions and extinctions, as it can remove local species and make habitats more prone to be invaded (Rahel 2002). The interactions that can occur from the three mechanisms are not easy to disentangle, but their relative importance can be accounted by looking over species list generated by studies and technical reports over a period of time, computing their similarity change.

Organizing and computing similarity data it is easy and it's one of the strongest points of using this framework to assess impacts on biodiversity, it result in an index easy to assimilate for overall public. Another strong component on this framework is to set in motion the use of data, taxonomic and basic ecology (diet, reproduction and growth) which could be retrieved from monitoring, technical reports, museum inventories and academic works. All those data could be efficiently used to quantify homogenization process in data-deficient regions (Neal *et al.* 2009). Obviously, many authors showed limitations on the scientific use of technical report data (e.g. Colwell and Coddington 1994, Fagan and Kareiva 1997, Cadotte *et al.* 2006) however, the benefits are obvious when simple data is better than none, even if scales (e.g. spatial and temporal) and taxonomic resolution were not designed to

explicitly assess homogenization. Even with some limitations due to unplanned data samples, the use of those kind of data are useful for scientific research as it can be transformed or adapted and should be used (Fagan and Kareiva 1997, Moreno and Hallfer 2010, Petesse and Petrere 2012). Analyzing the data we have through technical reports on infrastructure buildings is of fundamental importance, to prevent unwanted changes and for successfully managing biological systems. They become even more important because they allow us to evaluate impacts through temporal series because aside from potential impacts that have been demonstrated to occur in short-term (Dudgeon *et al.* 2006, Strayer 2012 and references therein) many alterations on freshwater might be causing changes (directly or indirectly) that will be perceived only in the long-term, for example, its common to non-native species (e.g. Strayer *et al.* 2006; Vitule *et al.* 2012b and references therein) to not directly and immediately become problematic (Crooks *et al.* 2011, Essl *et al.* 2011). Thus using those inventories we could identify some underlying mechanism of fish assemblages changes that leads to homogenization process, associated with human effects along temporal and spatial scales, even though they are logical to occur (Strayer 2012). But haven't be assessed because few long-term datasets have been sampled in a consistent way (Magurran *et al.* 2010) and models of species abundance are focused on spatial rather than temporal (Magurran 2007) and also because sometimes the effects (*i.e.* impacts) are transient and designating them as "desirable" can be in some cases a consequence of subjective analyses (Vitule *et al.* 2009, 2012b, Lapointe *et al.* 2012).

Homogenization metrics quantifies similarity changes in pairwise comparison of species pool on two or more biotas in at least two different times. Efficient tools are similarity metrics, like Jaccard's coefficient for presence/absence data (Villéger

and Brosse 2011) and Bray-Curtis or Morisita's index for species abundance (Winter *et al.* 2008, Pool and Olden 2012). A Multivariate Ordination analysis as NMDS (non-metric multidimensional scaling) could also be used to show graphically the similarity variation (Petesse and Petrere 2012, Vitule *et al.* 2012a).

The homogenization concept, quantitative estimates and models can be an important and effective approach to measure impacts, because anthropogenic stressors involving landscape transformation are increasing worldwide and, because globally there's a need for restoration and mitigation of future impacts on freshwater ecosystems. For example, regulation of flow regimes by dams (Nilsson *et al.* 2005, Poff *et al.* 2007), land use (Hascic and Wu 2006, Scott 2006), stocking of non-native species (Gozlan 2008) and water withdrawal (Hauer and Lorang 2004, Nilsson *et al.* 2005, Deacon *et al.* 2007) all with many potential consequences for aquatic biota, environment and future human generations.

### **The importance of homogenization framework**

Fish assemblages distinctiveness decrease were already perceived and recorded globally (e.g Rahel 2000, Taylor 2004, Olden *et al.* 2008, Watanabe 2010, Petesse and Petrere 2012, Vitule *et al.* 2012a, Baiser *et al.* 2012). Although spatial-temporal scales and diversity magnitudes were different among studies, results produced show how biotic homogenization is widespread and the magnitude and complexity of it, needs to be better explored on this New Pangea (Baiser *et al.* 2012). We argue that in a time where homogenized biotas are becoming common (McKinney and Lockwood 1999, Baiser *et al.* 2012), homogenization assessment on fish assemblage should be more employed and used to evaluate impacts by man-made hydrological infrastructure. In general, infrastructure towards human well-being

contributes to non-native fish establishment and extirpation of endemic species, ecotypes and/or populations (Rahel, 2007). Ultimately leading to a decrease in biological differences (e.g. taxonomic, genetic and/or functional) among naturally dissimilar biota (McKinney and Lockwood 1999, Rahel 2002, Olden *et al.* 2010, Olden 2006). Thus infrastructural engineering or other anthropogenic impacts are an important environmental change that occurs worldwide (Rahel 2000, Olden *et al.* 2008, Taylor 2010, Watanabe 2010, Vitule *et al.* 2012a). For example, one important way of altering hydrological features and disrupting native assemblage is through connectivity enablement or restriction, and this has not received proper attention during environmental impact studies of planned dams and other hydrological structures (Vitule *et al.* 2012a). Renewing the attention is important because there has been an increase in the number of dams, (Nazareno and Lovejoy 2011, Finer and Jenkins 2012) that with reservoirs formation facilitate the invasions process. Reservoirs are more prone to be used by humans than other natural water bodies , it also contributes to subsequent invasions acting as ‘stepping stones’ to natural lakes or other river parts, because it reduce landscape distance (Havel *et al.* 2005; Johnson *et al.* 2008). Structures can also connect distinct areas affecting unpredictably the freshwater fish fauna that was previously subject a multiplicity of physiographic barriers, for example when it floods waterfalls that works as ecological filter for many fish species (Vitule *et al.* 2012a).

Here with the aim to briefly review the importance of homogenization for freshwater fish conservation and research. Highlighting the quantification and monitoring of process when planning hydrological structures and after it's been built through rescue of technical reports and scientific studies using simple similarity metrics.

## Dams and fish passages

For around 5,000 years, water-retaining structures have been built to ensure water availability for domestic and agricultural purposes. Nowadays, over 47,500 dams fragment/block almost half of the world's river network (Nilsson *et al.* 2005). The belief that increasing irrigation and electricity production cause development and reduce poverty has led countries and international agencies, such as the World Bank, to investment in dam construction (World Commission on Dams 2000). Although the significant benefits mentioned above, impoundments affect flooding and flow patterns, sediment transport, trophic structure and species composition (Wellmeyer *et al.* 2005, Allan and Flecker 1993, Hoeinghaus *et al.* 2008, Moyle and Mount 2007, Rahel 2007).

This environmental change that occurs near dams homogenizes the habitat and would tend to homogenize reservoir and riverine assemblages. When distinct riverine areas with microhabitats are flooded, their biota is replaced by cosmopolitan lentic species (Rahel 2002, Johnson *et al.* 2008). The species turnover increase similarity between areas and lead to fauna homogenization process. While it seems logical, this issue has been sparsely accessed (Marchetti *et al.* 2006, Olden *et al.* 2010). Sided with habitat homogenization, reservoirs are an important way of non-native species introduction and dispersal, because native assemblage disruption increases establishment success of non-natives fishes (Moyle and Light 1996a, b, Havel *et al.* 2005, Johnson *et al.* 2008, Petesse and Petrere 2012, Vitule *et al.* 2012a). Reservoirs are also targets of compensatory and economic politics that promotes aquaculture with exotics (Leprieur *et al.* 2008, Strayer 2010) and has high affinity with human activities, for example sport fishing where more exotic species are introduced in the system. So when comparing regions with high incidence of



dams, we would expect to find the same cosmopolitan and lentic species together with a group of human related introduced species, leading to landscape level of homogenization.

Fauna homogenization may also occur by altering hydrologic connectivity (*sensu* Pringle 2001) between neighboring aquatic habitats. Dams reduce connectivity, being an untransposable obstacle, preventing fish migration in both ways and affecting recruitment that might sustain some species populations (Agostinho *et al.* 2007). The barrier coupled with reservoir homogenization would change composition similarity between areas as some populations might disappear due to lack of migration and the turnover that happens on impounded area.

A main concern of authorities and overall public with river fragmentation by dams is the obstruction of migration routes. Fish passages are the usual measures to address the problem, even though its efficiency has been questioned (Pompeu *et al.* 2012) as it mainly account the ascending part of the migration (Roscoe and Hinch 2010) and it is either biased toward some taxa (e.g. Salmoniformes) or to characteristics like, large body and economic importance (Agostinho *et al.* 2002). Homogenization framework and fish passage can be integrated if we consider the passage as selective increase in connectivity, a new route for downstream fauna to upstream area. Natives or non-natives that would not reach upper stretches due high water flow (Torrente-Vilara *et al.* 2011) or because of a geographical barrier (Vitule *et al.* 2012a), now are able to attempt with lower water flow of fish passages and expand their range to adjacent areas (Graça and Pavanelli 2007). Continued monitoring is essential to control possible introductions and possible impacts by non-native species (Makrakis *et al.* 2007). What may lead to a collapse in downstream fisheries, or losing of genetic pool resulting in genetic homogenization.

Hydrologic connectivity could also be enhanced by dams, impoundments can connect adjacent regions that were subject to different ecological filters for fish species, as waterfalls and water flow that sometimes represent biogeographic barriers (Vitule *et al.* 2012a), mainly allowing sedentary and low land fish to gain upstream access stretches, leading to loss of beta diversity as faunas start to mix (Torrente-Vilara *et al.* 2011).

Lastly, dams influence on composition and thus on homogenization process by altering river natural dynamic character of flow volume, timing and lateral and vertical connections (Poff *et al.* 1997, Bunn and Arthington 2002). Organisms and ecological functioning of river systems are highly influenced by water flow (Wiens *et al.* 2006, Torrente-Vilara 2011), changes in flow affects connections between river–floodplain systems: interfering in fluvial dynamics, migratory pathways, and habitat diversification, thereby reducing biodiversity in highly complex assemblages (Heiler *et al.* 1995, Frazier and Page 2006, Fullerton *et al.* 2010). Mims *et al.* (2013) reported that for multiple basins with controlled flow associated with dams, the ichthyofauna would change as flows decreases and becomes more predictable. Native species used to a high variable flow regime were being displaced in detriment of species with equilibrium strategy and the addition of non-native species, adapted to low variations in environment. These changes might increase a worldwide homogenization of freshwater fauna, trough introduction or survivor of species adapted to low flow variability and exclusion of native that were adapted to flow unpredictability.

General effects of dams to fish assemblages are almost the same independent of their size (e.g. barrier for migration, lotic habitat converted to lentic) and the effect they have on the fauna may change with river and dam size and

function (Poff and Hart 2002). Small dams usually target headwaters or streams of lower order of magnitude, affecting stream water volume and temperature. The two variables pose a considerable threat on how fish assemblages become structured after they construction (Cumming 2004).

Dams represent an optimal place to set in practice the framework about homogenization, in many countries before and after construction a monitoring work is realized that continues for a long period of time, thus create a temporal series needed for the framework. Although technical reports data often need to be adapted to verify influence those structures make on  $\alpha$ ,  $\beta$  and  $\gamma$  diversity in river network, data could be used to show trends of composition change, an impact that seems logical to occur, especially considering species introductions (Strayer 2012). Dams and associated are has concentrated a huge amount of studies about species auto-ecology what also helps assessing functional homogenization.

This idea has been shyly put in practice, two works in Neotropics assessed homogenization process using scientific and technical assemblage composition data to assess the impacts on beta-diversity those structure play. Petesse and Petrere (2011) explored the aging of a reservoir cascade group in a Neotropical river; they found that endemic species of each dam were being extirpated, while exotic species were introduced. As the reservoirs aged they found a trend to homogenization because non-natives were presented in multiples reservoirs and many of local of each reservoir were extirpated.

## **Transpositions**

Water demand increases worldwide, but neither water nor demand is equally distributed in time and space. To secure water availability we are diverting it from

one geographically distinct river catchment or basin to another catchment or river. (Vörösmarty *et al.* 2000, Oelkers *et al.* 2011). Such diversions are called “interbasin water transfers” or transpositions (Davies *et al.* 1992) and are common solution to address world’s water distribution crisis (Lynch *et al.* 2011).

The channels or tunnels created to divert water increases connectivity between rivers networks, allowing the dispersal of species between aquatic environments that without stream capture or geological events would be rare considering intrabasin or impossible considering interbasin connections (Lynch *et al.* 2011). New dispersal routes have potential to alter the pattern of species distribution and diversity (Strayer 2012). Trough homogenization framework we can evaluate the effects on diversity between areas connected through transpositions, by comparing their faunas before and after construction and further assessments to verify impacts that might be caused by the introduction of novel species on both environments, since initial invasion of some species is followed by a lag time until the populations of non-natives become successful established and the impact to be fully realized (Weyl *et al.* 2009). For example on a transposition in South Africa, a predator has changed macro invertebrate diversity. Rivers where it has established, only resilient taxa to the predatory impact remained (Kadye and Booth 2012). Other predatory species are now known to have made native species adjust their habitat range, being locally extirpated in some areas (Russel 2011). Fauna exchange can be evaluated using inventories and museums collections to establish pristine faunas that can be compared with sampled in locus present fauna. Contrary to what happen in dams where there is a transformation of lotic in lentic, on diverted waters we would expect that the fauna exchange is compromised by native species of each basin other than

translocated species from other regions of the world (Cambray and Jubb 1977), thus increasing similarity more regionally than globally.

## Conclusions and perspectives

Given the major importance of freshwater biodiversity and the severity of human impacts that are leading to a rapid impoverishment of freshwater biotas, we must focus on metrics and frameworks that are easy accessible to quantify impacts on said biodiversity. Homogenization is a tool for conservation and should be encouraged to quantify the nature and extent of human impacts on biodiversity (Olden *et al.* 2010), for example in relation to habitat alteration and/or water quality degradation and species introductions.

The framework rescues, updates and makes more accessible historical datasets of species composition, because academics and technical reports are rescued, giving values and use to well-done inventories other than be junk drawers. Inventories, on many countries, are mandatory by environmental agencies when building hydrological structures, and are a precious source of information. Inventory obligation before hydrological construction would be important to quantify biodiversity and long term impacts. All species lists produced by works mentioned above can, with taxonomic validations and data transformation, usually abundance to binary data, be used to quantify homogenization and given the context be interpreted to identify the driver of composition changes. For example, Vitule *et al.* 2012 verified homogenization between adjacent ecoregions, where a biogeographic filter was disrupted. On the context the 10% increase on similarity was due to increased connectivity that by species addition or extinction. The example also illustrates that this framework encompass mainly observational studies, which without technical works and reports, requiring long term sampling, what is unlikely to be sustained by academy alone, due to low financial investment in long term research acting as a barrier to do reliable monitoring (Man *et al.* 2004).

The framework can be powerful when studying hydrological structures because those structures are studied for many years in regular intervals producing temporal series and reliable diversity account. Temporal patterns is a main goal of biotic homogenization as it helps on highlight long term drivers of homogenization, for example impacts by non-natives that occurs after a lag time (Olden *et al.* 2010). Temporal series become useful to project future changes on aquatic ecosystems, being impacted by humans. For example Petesse and Petrere 2012, rescuing inventories and recording introduction and local extirpation in a dam series, noticed biotic differentiation that is projected to become homogenization, because non-native are becoming widespread, increasing dams to become more similar to each other. Concerning dams and water withdrawal, it represents an intense field to be developed since energy production is on demand worldwide. More dams and water withdrawal will be needed for cooling thermoelectrics and nuclear power plants increasing water withdrawal and manipulation by 18 to 24% (Mcdonald *et al.* 2012).

The framework could be simple but has a few restrictions that we should keep in mind. It's hard to make predictions on places where diversity is not fully known what creates uncertainty on species identity and difficult on establish what would be the native fauna, that could be partially solved out with recent methodologies to biodiversity assessment (Bellier *et al.* 2012). Taxonomic assessment might be easily solved with inventories, but functional and genetic evaluation of species in regions with high diversity is not an easy task too, as there is a tendency to study large bodied and economically important species (e.g. Braga *et al.* 2012), and there is a major lack of homogenization studies in poor regions of the world (Olden *et al.* 2010, Baiser *et al.* 2012). Characterizing functional diversity and its homogenization play an important role, as we replace ecological specialist by the same widespread

generalist, these might reduce ecosystem functioning, stability and assemblage resistance to environmental changes (Tilman *et al.* 1997, Sankaran and McNaughton 1999). While the understanding how life history traits truly quantify functional diversity isn't completely elucidated, its proxy has been used to quantify functional homogenization (Marchetti *et al.* 2004, Vila-Gispert *et al.* 2005, Olden and Poff, 2006) and improvements should be done on this direction, linking the traits and its effects to the ecosystem (Gosselin 2012). Improving our ability to link traits with ecosystem functioning would prove useful for conservation management, it would allow agencies to prioritize areas with high functional diversity than richness, as high richness might incur in high functional redundancy (Devictor *et al.* 2010), thus preserving multiple ecosystem functions.

As a take home message, we plea for conservation professionals to regard engineering feats as primary drivers of biotic homogenization, exploring how already built structures affect fish assemblage composition in different time and spatial scales with different biological organization levels. Management actions need to be built on this strong foundation when evaluating engineering feats, which have been designed without considering long-term environmental costs especially to fish assemblages. Therefore, reanalyzing data with a new framework offers essential insights and information in favor of the conservation of highly imperiled freshwater fauna, impacted by human activities (Dudgeon *et al.* 2006, Olden *et al.* 2010) in broader biodiversity crisis aspect, the homogenization of world's biota. Explicit considering the scales, context and the identity of the group being studied, we can better detect its mechanism and propose new and more robust conservations plans and evaluation the ones already in action.



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## **CAPÍTULO 2: HOMOGENIZATION OF FRESHWATER FISH FAUNAS AFTER THE ELIMINATION OF A NATURAL BARRIER BY A DAM IN NEOTROPICS.**

## **CAPÍTULO 2: HOMOGENEIZAÇÃO BIÓTICA DE PEIXES DULCÍCOLAS APÓS A ELIMINAÇÃO DE UM BARREIRA NATURAL POR UMA BARRAGEM NA REGIÃO NEOTROPICAL.**

As seções resumo, introdução, métodos, resultados, conclusão e referências deste capítulo serão apresentados no corpo deste artigo. O artigo se encontra na forma qual foi publicado durante o mestrado no periódico *Diversity and Distribution*.

**\*\* Nota sobre autoria:** Este capítulo foi um processo iniciado durante a graduação através da Iniciação Científica, sendo o projeto concebido e desenvolvido pelo Orientador, e que acabou por virar tema desta dissertação. A minha participação foi fundamental, ativa e efetiva durante toda a concepção do manuscrito, e como questão de justiça decidimos por manter como 1º Autor quem concebeu e evoluiu a ideia e realizou grande parte das análises. Devido a toda minha participação efetiva durante a produção e de esta ter inspirados os demais capítulos, este capítulo se encontra na dissertação.

**\*\*\*** Ao final do artigo se encontra as contribuições efetivas dos autores.



# Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics

Jean Ricardo Simões Vitule<sup>1,2,3\*</sup>, Felipe Skóra<sup>2,3</sup> and Vinícius Abilhoa<sup>2</sup>

<sup>1</sup>Laboratório de Ecologia e Conservação, Departamento de Engenharia Ambiental, Setor de Tecnologia, Universidade Federal do Paraná, 81531-970 Curitiba, Paraná, Brasil,

<sup>2</sup>Grupo de Pesquisas em Ictiofauna, Museu de História Natural Capão da Imbuia, Prefeitura de Curitiba, Rua Prof. Benedito Conceição, 407, 82810-080 Curitiba, Paraná, Brasil,

<sup>3</sup>P.P.G. Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Brasil, Postal Code 19.031, 81531-980 Curitiba, Paraná, Brasil

## ABSTRACT

**Aim** We quantify biotic homogenization of fish fauna caused by the elimination of a natural barrier between two freshwater ecoregions. We also evaluated fish introductions by different mechanisms such as aquaculture, angling and the aquarium trade in the homogenization of fish assemblages. The relative importance of native extinctions in the homogenization process was assessed by simulating the exclusion of threatened species in the data set.

**Location** Paraná River, south-eastern South America.

**Methods** A fish species list of the Parana River Basin was organized in a subset of species distributions, according to pre- and post-introductions caused by the elimination of the natural barrier and by other mechanisms. Biotic homogenization was verified by the use of Jaccard's and Bray–Curtis's coefficients, Whittaker's beta diversity index, non-metric multidimensional scaling analysis (NMDS) and nonparametric tests.

**Results** For all subsets of species distributions, we observed an increase in the number of non-native species in common related to the introductions. Between 40 and 52% of the species currently present in the Upper Paraná Basin dispersed upstream from the Lower Paraná after the construction of Itaipu Dam, including at least 1 class, 2 orders, 4 families and 16 genera of fish. Jaccard's coefficient between the Upper and Lower Parana River increased by 6–7.5% only considering the Itaipu Dam influence and 10.5% considering all mechanisms of fish introductions. More than 50% of the increase in similarity was caused by the elimination of the barrier. Our results indicated functional homogenization related to large-bodied Siluriformes (catfish).

**Main conclusions** Itaipu Lake flooded a natural barrier and allowed hydrologic connectivity between the Upper and Lower Paraná River, and many fishes of the lower part of the river were able to colonize the upper stretches. The homogenization of the two assemblages between these adjacent aquatic regions was an unpredicted result of hydropower implementation. Introductions by dam can also shift longitudinal and latitudinal body size patterns (i.e. Bergmann's rule).

## Keywords

Biodiversity crisis, biogeography, dam construction, ecological filter, Parana River, water resources conservation.

\*Correspondence: Jean Ricardo Simões Vitule, Laboratório de Ecologia e Conservação, Departamento de Engenharia Ambiental, Setor de Tecnologia, Universidade Federal do Paraná, 81531-970 Curitiba, Paraná, Brasil.  
E-mail: biovitule@gmail.com

## INTRODUCTION

Biotic homogenization refers to a decrease in taxonomic, genetic and/or functional differences among previously distinct biota (Olden, 2006). Such homogenization can be caused by the introduction of non-native species that are often cosmopolitan or human-associated, and/or the loss of native species,

most of them rare, localized and endemic (McKinney & Lockwood, 1999; Rahel, 2002). The phenomenon of homogenization is complex and extends across all levels of biological organization and may integrate, in a synergetic way, many aspects of the current global environmental crisis such as the introduction of non-native species, extinction and extirpations of native species, biodiversity loss, climate change, habitat loss

and habitat alteration (Rahel, 2002, 2007; Olden, 2006; Rahel & Olden, 2008). Therefore, it is a major form of global biotic impoverishment, and biodiversity loss has been considered as an unacceptable environmental change (Rockström *et al.*, 2009; Stigall, 2010).

In general, studies about homogenization have explored the loss of regional biotic integrity or distinctiveness because of the introduction of widespread, cosmopolitan or human-associated species and/or the extirpation of rare, localized and endemic species (e.g. McKinney & Lockwood, 1999; Rahel, 2000). Although many biologists have expressed major concern about this phenomenon, the extension of this process is still poorly documented in developing nations, where like other conservation issues (see Myers *et al.*, 2000; Brooks *et al.*, 2006; Abell *et al.*, 2008), this topic is often misunderstood and underexplored. In aquatic ecosystems of megadiverse countries like Brazil, for example, only recent papers have mentioned it and brought the topic to light (e.g. Vitule, 2009; Gubiani *et al.*, 2010).

In aquatic ecosystems, recent papers have expanded the theoretical framework of biotic homogenization (e.g. Olden & Poff, 2003; Olden *et al.*, 2010; Taylor, 2010; Watanabe, 2010), where introduction has generally increased local richness, as the establishment of non-native species through translocations, stocking, fish-farmers, anglers and engineering installations outpaced the extinction of native species. However, there are exceptions, where the dispersal and establishment of non-native species had destructive impacts on endemic biota (Rahel, 2002, 2007; Vitule *et al.*, 2009).

The level of biotic homogenization may be influenced by a great number of ecological characteristics, such as habitat conditions (Lambdon *et al.*, 2008; Qian *et al.*, 2008), the species involved (Rahel, 2000; Qian & Ricklefs, 2006), time after introduction and human interventions (Olden *et al.*, 2005; Smart *et al.*, 2006). In human-altered ecosystems, the removing of geographic constraints responsible for habitat isolation and dispersal limitations, for example, can provide a variety of pathways by which aquatic species can successfully invade another biota. The establishment of non-native fishes is more probable into altered system, where native assemblages have been disrupted (e.g. Moyle & Light, 1996a,b; Johnson *et al.*, 2008), such as those caused to community structure following river impoundment.

Dams can reduce hydrologic connectivity between neighbouring habitats or conversely enhance connectivity by allowing the dispersal of fish into systems outside of their natural range (Havel *et al.*, 2005; Johnson *et al.*, 2008). Reservoir construction, for example, may contribute to biotic homogenization through habitat homogenization and circumventing natural biogeographical filters (Rahel, 2002, 2007). In South America, the potential elimination of natural obstacles to fish movement has not received sufficient attention during environmental impact studies to date for many planned hydro-power dams (Júlio *et al.*, 2009).

This paper aims to quantify biotic homogenization of fish fauna caused by the flooding of an isolation mechanism

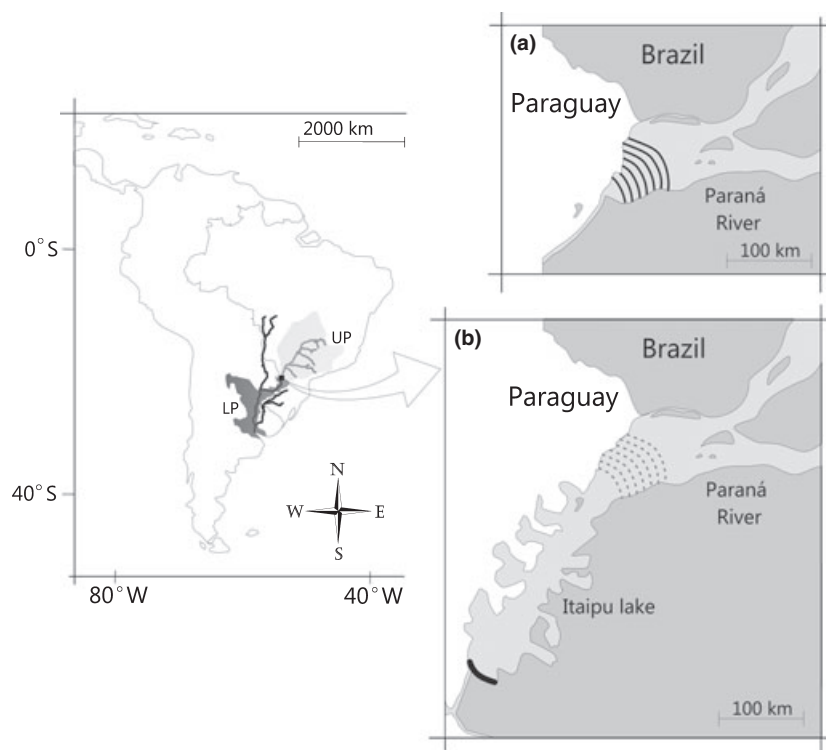
between the Upper and Lower Paraná River aquatic regions. The Itaipu Reservoir, located in the main channel of the Paraná River between Brazil and Paraguay, was completed in 1982, and it is one of the world's largest power plants. Itaipu inundated Sete Quedas (or Guaira) Falls, a so-called natural barrier between the Upper and Lower Paraná River regions. It is conceivable, however, that this barrier acted as an important 'ecological filter' instead of 'natural barrier', being quite impermeable for most species, but did not represent an absolutely insurmountable obstacle to the dispersion of migratory fish in periods of exceptional floods. According to Agostinho *et al.* (2007) and Júlio *et al.* (2009), in years of very high discharge, individuals of large migratory species such as *Salminus brasiliensis*, *Pseudoplatystoma corruscans*, *Piaractus mesopotamicus* and *Zungaro jahu* were able to cross the natural barrier in both directions, suggesting that the populations were not isolated to gene flow among regions (e.g. Bignoto *et al.*, 2009). Until now, only Langeani *et al.* (2007), Júlio *et al.* (2009) and Gubiani *et al.* (2010) have accessed the issue of species movement into the Upper Paraná River's aquatic environments after the elimination of the barrier created by the Itaipu impoundment. Although these papers are very relevant, there has not been previous concern about other changes in faunal similarities caused by the elimination of the barrier between the two regions. Further, previous work did not attempt to isolate the effect of the dam construction to that of introductions caused by different mechanisms such as aquaculture, angling and the aquarium trade between the aquatic regions. In other words, there is no framework to holistically understand biotic homogenization and its consequences.

## METHODS

### Study area

In south-eastern South America, the La Plata River Basin comprises a wide area of over 3.1 million km<sup>2</sup>, covering an extensive part of Argentina's continental territory, south-east Bolivia and the southern part of Brazil, Paraguay and Uruguay. The Paraná River is the largest sub-basin, constituting 48.7% of the La Plata Basin's overall surface area. The Paraná River is formed by the joining of the Grande and Paranaíba Rivers, and it is considered the 14th longest river in the world (4695 km).

The Paraná River flows north-south into the La Plata River in northern Argentina, draining most of the south-central part of South America from the Andes to the Serra do Mar near the Atlantic Ocean (Agostinho *et al.*, 2004). According to Bonetto (1986), the Sete Quedas (or Guaira) Falls, now flooded by the Itaipu impoundment, formerly constituted a natural barrier that separated two distinct ichthyofaunistic regions: the Upper Paraná (900,000 km<sup>2</sup>), almost completely inside Brazilian territory, and the Lower Paraná (or Parano-Platense ichthyofaunistic Province *sensu* Bonetto, 1986), with  $1.7 \times 10^6$  km<sup>2</sup> (excluding the Uruguay River) (Fig. 1). These two provinces are similar and coherent to the Upper and Lower Paraná ecological units proposed by the 'Freshwater Ecoregions of the



**Figure 1** The La Plata River system formed by the Paraná, Paraguay and Uruguay River basins. (a) The Sete Quedas Falls (black lines) formerly constituted a natural barrier separating the Upper (UP) and Lower (LP) Paraná freshwater ecoregions. (b) The Sete Quedas Falls were flooded (slight grey dots) in 1982 by the Itaipu Impounded.

World' project (*sensu* Abell *et al.*, 2008; FEOW – <http://www.feow.org>).

### Data collection

The master fish species list with taxonomic status and distribution data for the freshwater ichthyofauna of the Parana River Basin was generated from Reis *et al.* (2003), López *et al.* (2005), Langeani *et al.* (2007), Júlio *et al.* (2009) and FishBase (Froese & Pauly, 2011). The taxonomic classification of species follows FishBase (Froese & Pauly, 2011). We only consider fish species that have a currently valid scientific name to avoid taxonomic problems and discrepancies, such as hypothetical species and synonyms still in use. Native species were regarded as those that occur in the region as a result of natural processes, whereas non-native species were considered those with established reproducing populations registered outside their natural range because of the direct introduction by different mechanisms (e.g. aquaculture, angling and aquarium trade) or 'natural' dispersal between adjacent aquatic regions after the elimination of the barrier (indirect human influence).

Functional homogenization of fish fauna assemblages was examined through the species most commonly available ecological characteristics: maximum recorded body length, migratory behaviour and trophic level. Data on life history traits of fish species were collected from FishBase (Froese & Pauly, 2011) and available literature.

The assessment of biotic homogenization in fish fauna assemblages between the Upper and Lower Paraná River was calculated separately for the fish data provided by Langeani

*et al.* (2007) and Júlio *et al.* (2009), since these authors present some differences in species distribution status (native vs. non-native) and cause of introduction (direct vs. indirect) in the upper parts of Paraná River.

The final species list was reviewed case-by-case, and a subset of species distributions and ecological characteristics was selected according to the following criteria: Lower Paraná River Basin before fish introductions (LBTI), Lower Paraná River Basin after fish introductions (LATI), Upper Paraná River Basin before fish introduction according to Langeani *et al.* (2007) (UBIL), Upper Paraná River basin before introduction according to Júlio *et al.* (2009) (UBIJ), Upper Paraná River after fish introduction (UATI), Upper Paraná River after fish introduction caused only by the Itaipu impoundment, according to Langeani *et al.* (2007) (UAIL) and Upper Paraná River after fish introduction caused only by the Itaipu according to Júlio *et al.* (2009) (UAIJ) (see Appendix S1).

### Data analysis

Jaccard's coefficient, which is used for quantifying community similarity and is commonly employed in the quantitative estimates of homogenization (e.g. Rahel, 2000, 2002; Olden & Poff, 2003; Taylor, 2010), was applied among the described subset of species distributions. Jaccard's coefficient of percentage similarity was calculated as follows:  $J_{x1, x2} = [a/(a+b+c)] \times 100$ , where  $x1$  and  $x2$  symbolize two freshwater sites with specific fish assemblages,  $a$  is the total number of species current in both  $x1$  and  $x2$ ,  $b$  is the number of species that occur

in  $x_1$  and do not occur in  $x_2$ , and  $c$  is the number of species absent in  $x_1$  and present in  $x_2$ . Jaccard's coefficient (expressed as percentage) was quantified as the change (differences) in similarity for each subset pairwise combination over a specified time interval: pre- and post-introductions caused by Itaipu impoundment (i.e. elimination of the barrier) and by the sum of all different mechanisms of non-native species introduction (i.e. aquaculture, stocking – legal or illegal, angling, ornamental/aquarium trade).

Because homogenization can be characterized by species loss as well as species additions (Olden & Poff, 2003), we also assessed the potential effects of species losses in the homogenization process. Effects of species losses were evaluated by simulating the exclusion of all threatened species and recalculating similarities. Even though the categorizations of threatened species (endangered, vulnerable and rare) made by Chebez (1999) and Machado *et al.* (2008) may not accurately reflect actual extinction risks, our intention was to compare the relative importance of introductions vs. extinctions of native species in driving patterns of homogenization to predict the worst possible scenario.

Differences in fish assemblages among each subset pairwise combination were also assessed using Whittaker's beta diversity index (turnover of species across gradients). The index value varies from 0 (identical faunas) to 1 (no species in common). Whittaker's index between pre- and post-introductions was compared by the Wilcoxon signed rank test and by box plots.

Our comparative analysis of fish assemblages' similarities among the subset of species distributions included a non-metric multidimensional scaling analysis – NMDS – (Clarke & Gorley, 2006) to display, in a two-dimensional plane, the variations of similarities among the described subsets. The NMDS multivariate ordination was performed on the presence/absence matrix of the subsets of species distributions and migratory behaviour using Jaccard's coefficient and on the continuous functional ecological characteristics data (maximum body length and trophic level,  $\log_{10}$ -transformed) using the Bray–Curtis similarity coefficient. We preferred to use the NMDS analysis over other ordination methods because it makes fewer assumptions about the nature of the data, it allows the use of any distance measure of the samples, and it also seeks to preserve the distance relationships among the samples in the low-dimensional ordination space (Clarke, 1993). Minimal connections among subsets of fish distribution were summarized by superimposing a minimum spanning tree on the NMDS ordination. The multivariate ordination analyses were performed using PAST version 1.9 (Hammer *et al.*, 2001).

The effect and magnitude of body length and trophic level were also statistically evaluated through a comparative analysis using Kruskal–Wallis one-way analysis of variance by ranks, the Wilcoxon signed rank test and box plots. All data were  $\log_{10}$ -transformed prior to analyses. Tests were performed to assess differences in ecological characteristics among fish assemblages and taxonomic orders between the Upper and Lower Paraná River before and after introductions. The

effect of migratory behaviour frequencies was assessed using chi-square test. All box plots and nonparametric tests were performed in the R software environment for statistical computing and graphics (R Development Core Team, 2008).

## RESULTS

The total data set consisted of 492 species from three classes, 13 orders and 43 families distributed in both aquatic ecoregions. The order with the highest richness was Siluriformes, having 199 species, followed by Characiformes (181 species), Perciformes (40 species) and Gymnotiformes (20 species). Of the total, 332 valid species were found to currently occur in the upper parts of the Paraná River, 264 being native and 68 (21%) non-native; In the Lower Paraná River, 299 occurred, being 292 natives and only 6 (1%) non-natives (Table 1).

Based on Langeani *et al.* (2007), our data showed that 52% of the non-natives species currently present in the Upper Paraná Basin dispersed from the Lower Paraná after the construction of Itaipu Dam. These species were distributed in 31 genera. Eleven (35%) of those already occurred in the Upper Paraná Basin, whereas 20 (65%) were exclusive to the Lower Paraná before the dam. When taking into account higher taxa, 1 class, 3 orders and 6 families that reached the Upper Paraná were also exclusive to the lower region before impoundment. When considering our data set in relation to Júlio *et al.* (2009), 40% of the non-natives species currently present in the upper basin reached the upstream regions after the elimination of the barrier. These species belonged to 25 genera. Nine (36%) already occurred in the Upper Paraná Basin, and 16 (64%) were exclusive to the Lower Paraná before the construction of the dam. Considering higher taxa, 1 class, 2 orders and 4 families that occurred exclusively in the Lower Paraná Region invaded the Upper Paraná (see Table 1 and Appendix S1).

**Table 1** Number of fish taxa in the Upper and Lower Paraná basin before and after introductions caused by the elimination of the barrier and by other mechanisms.

Taxa	Before introductions		After introductions	
	Lower Paraná	Upper Paraná	Lower Paraná	Upper Paraná
Class	3	1	3	2
Order	12	6	13	11
Family	40	27	42	38
Genus*	152	116 <sup>J</sup> /117 <sup>L</sup> (115†)	156	154
Species*	292	258 <sup>J</sup> /259 <sup>L</sup> (253†)	299	332

\*Numbers and status of native genus and species provided by Langeani *et al.* (2007)<sup>L</sup> and Júlio *et al.* (2009)<sup>J</sup> are different because those authors disagree on the identity of several species.

†Number of genera and species in common considering both lists (see Appendix S1).

**Table 2** Homogenization measures ( $\Delta J$ ) among the Lower and Upper Paraná subsets considering all fish taxa (left) and simulating the exclusion of threatened species (right).

		All fish taxa					Scenario excluding threatened species				
Lower subsets		Upper subsets									
After and before introduction		After introduction	<i>Ja</i> (%)	Before introduction	<i>Jb</i> (%)	$\Delta J$ (1)	After introduction	<i>Ja</i> (%)	Before introduction	<i>Jb</i> (%)	$\Delta J$ (2)
After	vs.	UAIJ	22.85	UBIJ	16.56	<b>6.29</b>	UAIJ	21.27	UBIJ	15.73	<b>5.54</b>
Before	vs.	UAIJ	22.88	UBIJ	16.53	<b>6.35</b>	UAIJ	21.78	UBIJ	15.79	<b>5.99</b>
After	vs.	UAIL	24.48	UBIL	16.77	<b>7.71</b>	UAIL	22.98	UBIL	16.06	<b>6.92</b>
Before	vs.	UAIL	24.52	UBIL	16.74	<b>7.78</b>	UAIL	24.46	UBIL	16.02	<b>8.44</b>
Before	vs.	UATI	27.03	UBIL	16.77	10.26	UATI	27.03	UBIL	16.06	10.97
Before	vs.	UATI	27.03	UBIJ	16.56	10.47	UATI	27.03	UBIJ	15.84	11.19
Before	vs.	UATI	27.03	UBIL	16.74	10.29	UATI	27.03	UBIL	16.02	11.01
Before	vs.	UATI	27.03	UBIJ	16.53	10.50	UATI	27.03	UBIJ	15.79	11.24
After	vs.	UATI	28.25	UBIL	16.77	11.48	UATI	26.69	UBIL	16.06	10.63
After	vs.	UATI	28.25	UBIJ	16.56	11.69	UATI	26.69	UBIJ	15.84	10.85

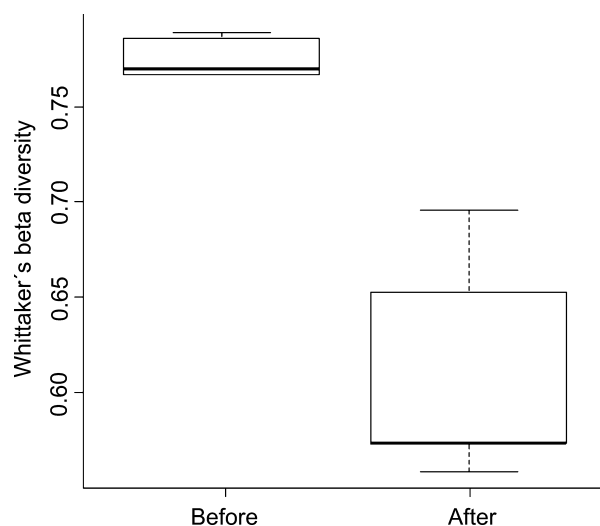
Jaccard's similarity coefficient (expressed as percentage) was calculated between the Lower and Upper subsets after (*Ja*) and before (*Jb*) introductions.  $\Delta J$  values are the respective changes in similarities after the event of fish introduction.  $\Delta J$  (1) – considering all fish taxa and  $\Delta J$  (2) – simulating the exclusion of threatened species.  $\Delta J$  bolder values show the homogenization (i.e. increase in similarity) in fish fauna assemblages between the Upper and Lower Paraná River after the elimination of the barrier by the impoundment.

There was an evident and significant increase in the similarity for all subset combinations in our quantifications (Table 2). Considering only fish introduction caused by the Itaipu, the similarity measures among the upper and lower basin increased from 16.53–16.77% to 22.85–24.52%, depending on the reference used (Langeani *et al.*, 2007 or Júlio *et al.*, 2009). In contrast, when evaluating all kinds of species introduction, the increase in similarity was from 16.53–16.77% to 27.03–28.25%, taking account the aquatic environments after the elimination of the barrier by the Itaipu impoundment. In the simulations excluding threatened species, the taxonomic similarities among the Upper and Lower Paraná Basin after impoundment, we found an increase from 15.73–16.06% to 21.27–24.46. When all kinds of species introduction were evaluated, values ranged from 15.84–16.06% to 26.69–27.03%.

As a further index of taxonomic homogenization, the turnover of species distribution subsets before and after incorporating introductions of non-native fishes dropped an average of 0.16 (Fig. 2). The analysis of turnover in fish species composition between pre- and post-introductions clearly showed a significant decrease in the distinctiveness of the fish fauna after introductions ( $Z = 45$ ,  $P = 0.0039$ ) (see Appendix S2).

Ordination revealed a distinct separation among the pre- and post-introduction subsets of species distributions and ecological characteristics, also indicating that similarity increased between the Upper and Lower Paraná Basin. The effect of elimination of the barrier and all mechanisms of fish introductions indicated taxonomical and functional homogenization (Fig. 3).

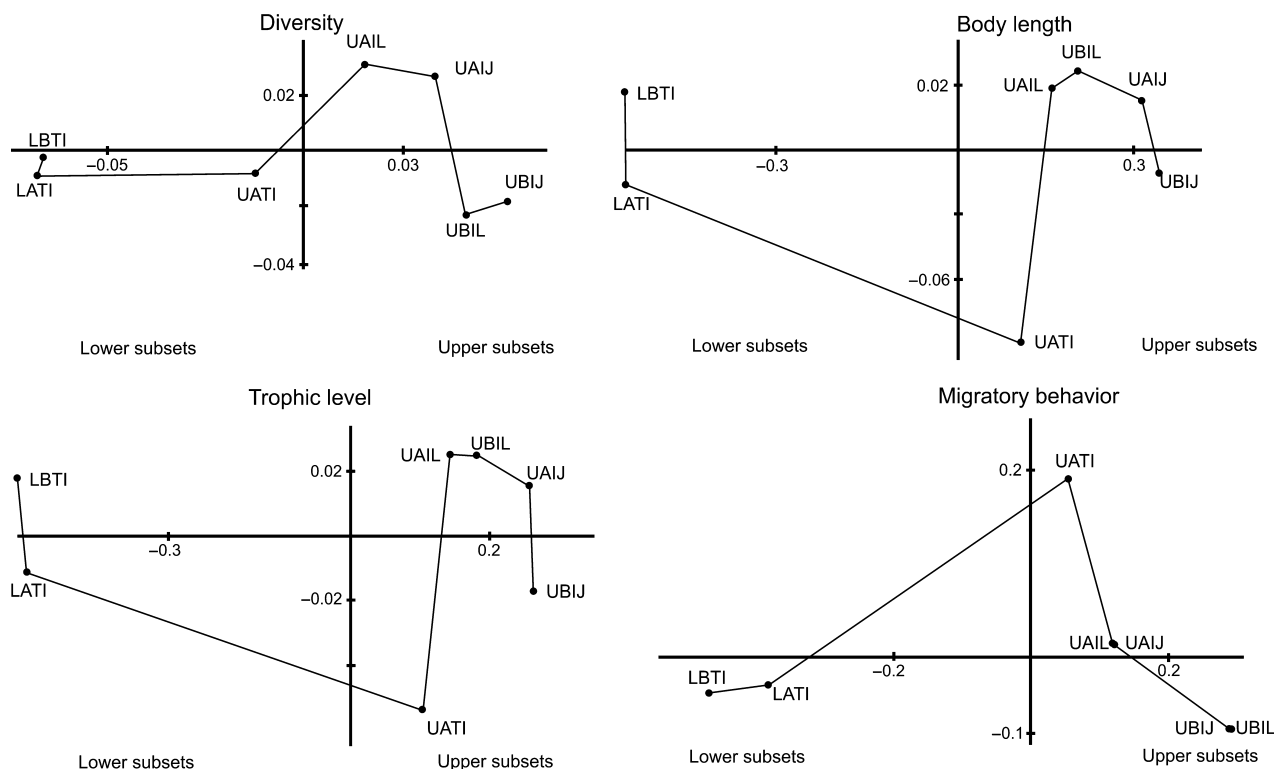
Nonparametric tests and box plots of ecological traits showed that larger maximum body length was the most



**Figure 2** Box plot comparing all subsets of species distribution before and after introductions of non-native fishes using the Whittaker's beta diversity index. Bold lines in the box are the median of the data. Boxes include 50% of the data; 75th percentiles are indicated in the top of the box (upper quartile), and the bottom of the box indicates the 25th percentile (lower quartile) of the data. Vertical lines extend to the upper and lower deciles (90th and 10th percentiles). Wilcoxon signed rank test showed a significant decrease in the distinctiveness of the fish fauna after introductions ( $Z = 45$ ,  $P$ -value = 0.0039).

important characteristic (or commonality) among the species that successfully colonized the upstream portion of the river. Statistical significance also found the Siluriformes phylogenetic influence on body size (Fig. 4). The effect of trophic level





**Figure 3** Ordination plot based on the non-metric multidimensional scaling analysis (NMDS, stress < 0.0001) using Jaccard's similarity coefficient of the Lower (LBTI and LATI) and Upper (UAIJ, UAIL, UBIJ, UBIL and UATI) Paraná subsets of the entire assemblage, considering species distributions (diversity), body length, trophic level and migratory behaviour. Each subset is joined using a minimum spanning tree.

( $H = 5.84$ ,  $P = 0.56$ ) and migratory behaviour ( $\chi^2 = 0.43$ ,  $P = 0.81$ ) revealed no statistical difference in all possible comparisons.

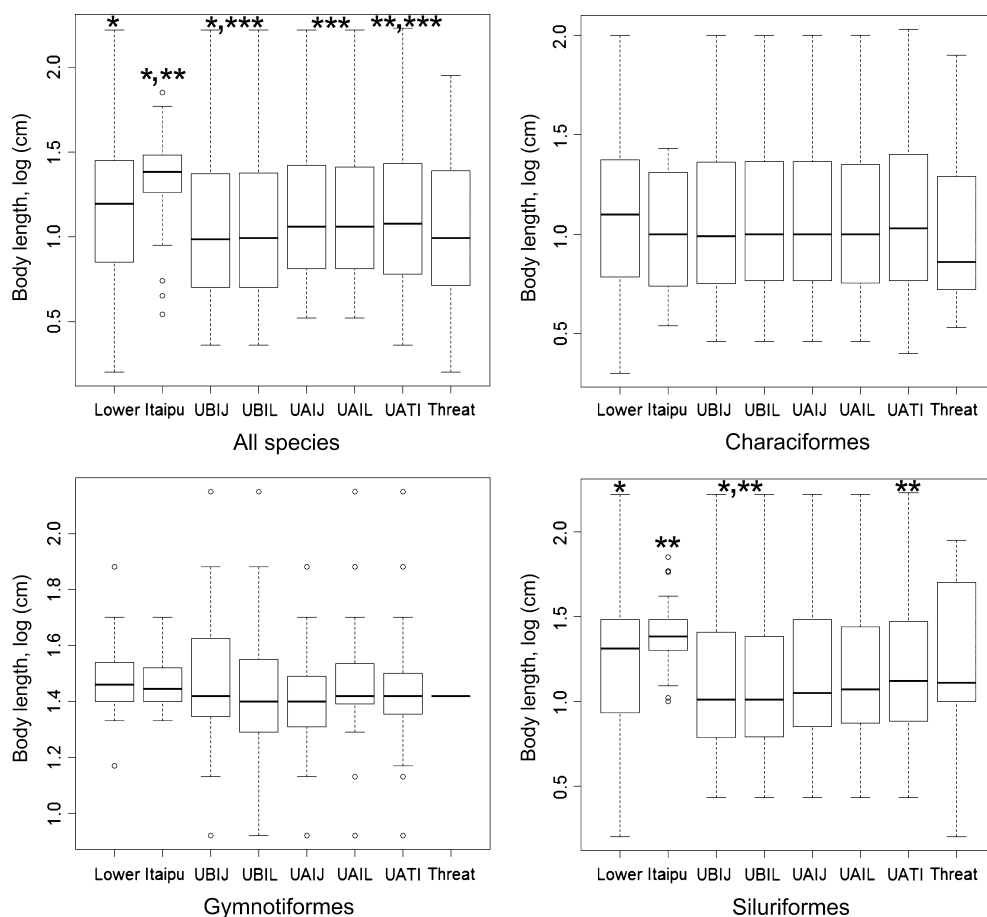
## DISCUSSION

In south-eastern South America, the Itaipu impoundment flooded a natural barrier between the Upper and Lower Paraná River, and fishes of the lower part of the river basin massively colonized the upper stretches. The homogenization that has been verified was due primarily to the unidirectional fish species advance to upper regions rather than the extirpation of threatened species. The biotic homogenization between these adjacent aquatic regions was an unpredicted and unquantified result of the hydropower implementation.

Notwithstanding the significant decrease in the distinctiveness of the fish fauna after introductions, our results also indicated that similarity between the Upper and Lower Paraná River increased 6–7.5% only because of the Itaipu's influence (which represented more than 50% of the increase in similarity between the upper and lower portions of the river was caused by the elimination of the barrier), and 10.5% was related to various kinds of fish introductions. This degree of homogenization was similar to similarity among 27 areas in Japan that increased an average of 9% (13.6 forms/area Watanabe, 2010) and larger than 7.2% average similarity from 48 states of the

United States (18.8 species/area Rahel, 2000), 1.2% average similarity from 13 provinces and territories in Canada (7.8 species/area Taylor, 2004; average similarity that decreased by 0.9% between 2000 and 2005 Taylor, 2010) and 3.0% among major drainages in Australian fish faunas (Olden *et al.*, 2008). Although the geographic scale and original species diversity were different among the studied areas, all results highlighted the magnitude and complexity of the homogenization process, as well as the potential dimension of the previously underexplored impacts.

Since scale can influence the community's degree of saturation (Davies *et al.*, 2011), we believe that our results were greatly affected by the spatial scale used, but they correspond to predicted scenarios at large scales, where homogenization is expected (Olden & Poff, 2003). Although species extirpations following fish introductions have rarely been detected at the large regional scale, population-level extinctions may occur at smaller spatial scales mainly when non-native species reduce the native species to a small population fragments in a few refuges (e.g. Leprieux *et al.*, 2006; Pelicice & Agostinho, 2008). In this respect, we believe that the underestimation of the real number of many small range extirpations (i.e. local extinctions in reservoirs by environmental change or by invasive species e.g. Pelicice & Agostinho, 2008) is almost certain. On the other hand, our results were very realistic from a biogeographical viewpoint



**Figure 4** Box plots comparing body length effects for all species ( $N = 492$ ), Characiformes ( $N = 181$ ), Gymnotiformes ( $N = 20$ ) and Siluriformes ( $N = 199$ ). Subsets organized according to the following criteria: Lower Paraná before introductions (Lower), fish introduced only by Itaipu impoundment (Itaipu), Upper Paraná before (UBIJ and UBIL) and after (UAIJ, UAIL and UATI) introductions, and considering only threatened species (threat). Bold lines in the box are the median of the data. Boxes include 50% of the data; 75th percentiles are indicated in the top of the box (upper quartile), and the bottom of the box indicates the 25th percentile (lower quartile) of the data. Vertical lines extend to the upper and lower deciles (90th and 10th percentiles). Significant differences were observed in all species ( $H = 17.55$ ,  $P < 0.01$ ), and Siluriformes influence on body size ( $H = 38.01$ ,  $P < 0.01$ ). Subsets were pairwise compared, and statistical significances were indicated (\* $P < 0.001$ , \*\* $P < 0.01$ , \*\*\* $P < 0.05$ ).

(especially regional) and will stimulate new research in the future about this new paradigm. Even though obtaining accurate small-scale data for these two regions is very difficult and it is beyond the scope of the present study, we believe that this kind of small-scale homogenization investigation needs to be addressed. In general, the human-mediated introduction and extinction processes act at different temporal scales, where species extinctions might take many decades to come to completion, and such time-lags could generate a huge debt in extinctions that will be paid in the future (Sax *et al.*, 2002; Sax & Gaines, 2008).

In addition to the taxonomic homogenization process, our results on the influence of introduced species' ecological traits using multidimensional analysis also revealed that similarity increased between the Upper and Lower Paraná Basin. In contrast, central tendency analysis demonstrated that only body size showed significant differences before and after the massive faunal mixing, and trophic level and migratory

behaviour were less likely to predict the functional implications of community changes. Our results also illustrated that those ecological traits were not useful tools to characterize species that were extirpated by simulating the exclusion of all threatened species in the homogenization process. Such observations are related to the fact that environmental threats on small- and large-bodied freshwater fishes are very complex, and it is not easy to predict the real species extinction risk in relation to simple or individual life history traits (Olden *et al.*, 2007).

Large body size was the most important ecological trait that can predict successful colonizers. In general, successfully established non-native fishes tend to have larger sizes than native fish species (Vila-Gispert *et al.*, 2005; Ribeiro *et al.*, 2008), which can be explained by the fact that body size is a crucial ecological characteristic associated with growth, fecundity and age at maturity, competitive success, mortality rates, longevity, trophic position and the functioning of food webs



(Layman *et al.*, 2005; Olden *et al.*, 2007). Our results also showed that size differences were influenced at least in part by phylogeny, due primarily to the unidirectional large-bodied Siluriformes that advance to upper regions after Itaipu impoundment. We believe that Siluriformes were significantly over-represented because they are naturally one of the most diverse groups of vertebrates, especially in the Neotropics. This group also constitutes the main fish component of the Parana River basin, and even before any fish introductions this order already accounted for more than 40% of species. Thus, the natural richness of this group of fish could not prevent new massive catfish invasions. Additionally, our results indicated that indirect human introductions by dam can also shift longitudinal and even latitudinal body size patterns especially in the southern hemisphere (i.e. Bergmann's rule, Blanchet *et al.*, 2010).

Considering the ecological characteristics examined, migratory behaviour and trophic level seem not to be good predictors of invasion success or even represent a real barrier to invasion of the species that colonized upstream reaches. Migratory behaviour frequencies did not differ in both assemblages probably because the same groups of characins (Characiformes) and catfish (Siluriformes) that were evaluated are migratory and require the same kind of spawning, nursery and feeding habitats to complete their life history (Agostinho *et al.*, 2003). Similarly, our trophic level statistical approach did not detect differences among the upper and lower subsets before and after introductions, even though introduced species are expected to occupy an ecological niche unoccupied by the native community (Moyle & Marchetti, 2006), altering the community trophic structure of the area invaded and causing them to become homogenized in functional scale (Olden *et al.*, 2004). This topic clearly deserves further investigation, and different approaches may lead to stronger predictive models of invasion success. Indeed, we believe that comprehensive analyses on the patterns of food resource use (trophic guilds) and partitioning are needed to clarify how the naturalized non-native invaders interact with native species.

Our study is an initial assessment to understand the changes that have occurred in the Parana River Basin after the dispersal of fish into aquatic systems outside of their natural range. We would emphasize that not much effort has gone into looking for homogenization or the elimination of ecological filters and its consequences in the Neotropical region, and only recently dam construction was highlighted as a potential source of homogenization between freshwater ecosystems because of the removal of natural barriers, stocking programs and other sources of human introductions (Agostinho *et al.*, 2010; Torrente-Vilara *et al.*, 2011). How the ongoing homogenization of fish communities will exactly remodel the aquatic community structure and function remains largely unknown. Biotic changes in aquatic ecosystems by aquaculture, aquarium species additions, angling and engineering feats are increasing very fast in developing countries, and their impacts and consequences are still largely underexplored.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** List of fish species presence–absence data in the aquatic ecoregions of Lower and Upper Paraná River before and after fish introductions.

**Appendix S2** Whittaker's beta diversity index ( $\beta$ ) comparing all subsets of species distribution before and after introductions of non-native fishes.

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## BIOSKETCHES

**J.R.S. Vitule** is interested in ecology and management of invasive species. His research focuses on the conservation of the endemic freshwater fishes of the Atlantic rain forest, and the management of non-native fish species that threaten their survival.

**V. Abilhoa** is the curator of the Fish Collection of the Capão da Imbuia Natural History Museum. His research includes taxonomy, inventory of fish species and aquatic ecosystem diversity.

**F. Skóra** is a master student interested in freshwater ecology, especially fish invasions and homogenization.

Authors contributions: J.R.S.V. conceived and developed the idea for the present study; J.R.S.V. and V.A. conducted the data analysis; J.R.S.V., F.S.N. and V.A. made databases compilation and wrote the manuscript.

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**CAPÍTULO 3: REVISITING DARWIN'S NATURALIZATION HYPOTHESES:  
EVALUATING A NATURAL EXPERIMENT OF MASSIVE FRESHWATER FISH  
INVASION ON A DISRUPTED FILTER.**

**CAPÍTULO 3: HIPÓTESE DE NATURALIZAÇÃO DE DARWIN: AVALIANDO UM  
EXPERIMENTO NATURAL DE INVASÃO MASSIVA DE PEIXES DULCÍCULAS  
APÓS A ELIMINAÇÃO DE UM FILTRO ECOLÓGICO.**

O artigo está formatado para a seção 'Letter' do periódico *Ecology Letters*, contendo entre 2500 e 3000 palavras. Para fim da dissertação este limite foi extrapolado.

\*\* O artigo Vitule *et al.* (2012b) é referência ao capítulo anterior desta dissertação, assim facilitando a consulta a mapas e ideias contidas na capítulo anterior necessária para o entendimento deste.

## REVISITING DARWIN'S NATURALIZATION HYPOTHESES: EVALUATING A NATURAL EXPERIMENT OF MASSIVE FRESHWATER FISH INVASION ON A DISRUPTED FILTER

Felipe Skóra<sup>1,3</sup>

Vinícius Abilhoa<sup>2</sup>

André Andrian Padial<sup>3</sup>

Jean Ricardo Simões Vitule<sup>1,2,3</sup>

<sup>1</sup> Laboratório de Ecologia e Conservação, Departamento de Engenharia Ambiental, Setor de Tecnologia, Universidade Federal do Paraná, 81531-970, Curitiba, Paraná, Brasil; <sup>2</sup> Grupo de Pesquisas em Ictiofauna, Museu de História Natural Capão da Imbuia, Prefeitura de Curitiba, Rua Prof. Benedito Conceição, 407, 82810-080, Curitiba, Paraná, Brasil; <sup>3</sup> P.P.G. Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná.

Correspondence:

Jean R. S. Vitule, Laboratório de Ecologia e Conservação, Departamento de Engenharia Ambiental, Setor de Tecnologia, Universidade Federal do Paraná, 81531-970, Curitiba, Paraná, Brasil.

Telephone: +5541 3361 3482

E-mail: biovitule@gmail.com

## Abstract

Freshwater ecosystems are considered one of the most imperiled by biological invasion. While being able to understand and predict invasion success had been a long term goal of biological invasions studies. Experimental approaches are needed to validate some proposed theories concerning establishment success. Using data from a quasi-natural experiment where the elimination of a vicariant barrier for fishes mixed two distinct faunas, especially allowing a massive unidirectional fish invasion, to happen on downstream-upstream direction. We investigate this regional scale fact under the optic of Darwin's naturalization hypothesis. Invading species would have reduced chance to establish if a taxonomic/functional related native were present recipient area. The major advance this study provides is reducing the 2 major sources of errors of previous studies using freshwater fish fauna. We know realistically the potential invader donor pool, and use functional traits to quantify niche use, as taxonomy may not reflect competition. Relatedness between the species pools were done through taxonomy and measure of 'alpha niche', the latter utilizing species most common functional traits available. The 'alpha niche' measures were also used through a conceptual model, the 'alpha niche' of an invader was compared one by one with the entire native community, to see how much of native community was similar to that invader. Conceptual models and taxonomical contingences tests shows no support for Darwin's hypothesis. However, considering the large scale analyzed. The order Characiformes showed on taxonomic testing, a signal that with some caution could be interpreted as confirmation. A high failure count of species with native congeners present, this demands further investigation. 'Alpha niche' metrics shows that distance from invader to the native species most functional similar agrees with Darwin's hypothesis, successful invaders were more dissimilar to native fauna than failed ones. Increasing our ability to measure traits related to competition and reducing scale to where biotic interactions matters, might reveal that the methodologies considering nearest species and the conceptual model to be effective predictors of invasion success.

## Introduction

Biological invasions and its impacts on freshwater are eroding local biodiversity faster than any natural process, and its being accelerated by anthropogenic activities (Pimm *et al.* 1995, Vitousek *et al.* 1996; Vitule *et al.* 2012a). Massive species interchange across their natural dispersal barriers has become a major modern human threat to freshwater ecosystems (Vitule *et al.* 2012a). Another threat exacerbated by humans are reservoirs and dams building, because it disrupt native faunas and alter the habitat increasing the invasion probability (Moyle and Light 1996a, Havel *et al.* 2005, Johnson *et al.* 2008). In this context of intense environment modification, being able to understand and predict which potential invasive species would be capable to establish and spread on an ecosystem, would be of extreme value to invasion management. Considering that global warming and human activities may offer new opportunities and pathways for introductions (Walther *et al.* 2009). Predicting becomes the major focus on invasion and conservation ecology (Hayes and Barry 2008, Strayer 2012).

Theories have been proposed to explain variations in invasion establishment success of exotic species (e.g. propagule pressure, enemy release, invasion meltdown, environmental tolerance and many others (extended review in Catford *et al.* 2009, Lowry *et al.* 2012); but generalizations about success chance of an invader to establish remains unclear, as studies about invasions shows variations in success across taxa and geographic regions (Blackburn and Duncan 2001; Tingley *et al.* 2010). While some theories needs a good amount of data, often unavailable, or based in factors that are difficult to quantify and/or measure worldwide (Strayer 2012). A common approach has been to seek proxy variables that could be easily quantified to measure invasion success. Proxies also must be tied to account the location it happened, the introduction event, the invader traits and ultimately with characteristics of the recipient assemblage, since the diversity of native assemblage may influence the success, even though it have been sparsely quantified in studies using species traits as predictor of establishment (Lockwood *et al.* 2007, Thuiller *et al.* 2010). One proxy is the taxonomic or phylogenetic relationships between invaders and the natural assemblage, as it attempts to quantify niche overlap and a possible biotic resistance trough competition, and also used to predict impacts of said invader (Ricciardi and Atkinson 2004, Thuiller *et al.* 2010). Thus knowing the

composition of the recipient assemblage could be used to predict which species will be able to establish, give in consideration the context dependence of biological invasions about propagule pressure, habitat integrity degree, etc (Simberloff *et al.* 2013).

The idea of using relatedness proxy been proposed by Darwin (1859), he postulated that naturalization of a non-native plant species would be less likely on assemblages in which there were close relatives of the invader. Darwin's rationalization is that closely related species would tend to occupy similar niches, survive under same environmental conditions, sharing similar traits, pathogens and predators. An invasive similar to a native would have their establishment chance lowered because it would compete for resources, suffer from predators and pathogens already present in the assemblage. Darwin also recognized another point of view, what became known as the pre-adaptation hypothesis in which exotic sharing traits with a native may confer a pre-adaptation mainly to abiotic factors facilitating establishment of the invasive species to the novel environment, this implies some degree of niche conservatism between related genera, or in other words, related genera due to its evolutionary history would show similar environmental needs (Wiens and Graham 2005, Diez *et al.* 2008).

Results of previous studies of Darwin's naturalization hypothesis have generated conflicting results, while some agree with the naturalization hypothesis (Ricciardi and Atkinson 2004; Jiang *et al.* 2010), others found that invasive species are more related with native assemblage, agreeing with the pre-adaptation hypothesis, or are under the expectation rates of null models (Daehler 2001; Ricciardi and Mottiar 2006; Diez *et al.* 2009; Tingley *et al.* 2011). These conflicting results can be explained by how the hypothesis were built and tested, how it compares the invasive species with the native assemblage, the phylogenetic (Proches *et al.* 2008) and spatial scale used (Carboni *et al.* 2012) and because the different metrics used on statistical tests (see table 1 in Thuiller *et al.* 2010). Due to this lack of concordance and multiple ways to tackle the same hypothesis, a unified approach was recently proposed by Thuiller *et al.* (2010) to assess Darwin's naturalization hypotheses. Ecologist should take in account the context of why the invasion happened, spatial and temporal scale since both are known to affect how we see 'relatedness' effects on biotic resistance (Davies *et al.* 2005, Lockwood *et al.*



2007), and when evaluating relatedness influence invasion success we should not only take taxonomical status (e.g. Duncan and Williams 2002, Ricciardi and Mottiar 2006) but account niche overlap through phylogeny or functional traits (also called ‘alpha niche’ approach) through metrics proposed by Thuiller and collaborators (2010).

Trying to address all the points mentioned above, we investigate Darwin’s naturalization hypothesis utilizing a ‘quasi-natural or natural experiment’. An observational experiment of a massive unidirectional fish invasion occurred from one site to another after a reservoir construction. The reservoir flooded Sete Quedas fall eliminating an important biogeographic and ecological filter connecting two distinct freshwater ecoregion of the world, Upper and Lower Parana, capturing in few days multiple species from lower to upper region into a novel environment (Vitule *et al.* 2012a), we seek to quantify invasion success through relatedness. We have a realistic database of the donor pool of invasive species that succeed and failed, that shared evolutionary history and inhabit the same river even that been separated by a vicariant barrier, so it’s less likely that we incur on the problem of overestimating success and underestimating failed invaders, what is a potential source of error. The donor pool is also sympatric with the native pool, so it is quite probable that congeners coexisted in time, instead of being totally novel because it was translocated from another continent. Knowing the donor pool allowed us to use common available characteristics and evaluate niche differentiation through functional dissimilarities, what have never been done considering fish invasions with this much diversity.

We evaluate the use of taxonomical and functional traits proxies to test Darwin’s naturalization hypothesis on the following ways, with our predicted results for each one.

- (I) Using taxonomic status: The presence of correlated taxa on a novel environment will decrease the establishment chance of a nonnative species than expect by chance.
- (II) A functional trait approach: species are analyzed through their functional characteristics (alpha niche *sensu* Thuiller *et al.* 2010). We expect that successful invaders would be more dissimilar to native assemblage than

failed invaders, in distance to nearest native and mean distance to native community metric.

- (III) With functional traits matrix approach, we conceptualize a new approach (described in details below). Using the similarity distance relationship of each potential invader to every species of invaded assemblage. We expect to occur three tendencies: (1) Invader being more dissimilar to most of the native assemblage (logarithmic curve). (2) Invader being similar to most of the native assemblage (exponential curve). (3) Invader being evenly similar and dissimilar to the entire community (Linear relationship). We expect, following Darwin's rationalization, that successful will show a higher frequency of logarithmic curves, invader being more dissimilar, and failed showing a higher frequency of exponential curves, being more similar to natives assemblage.

## Material and methods

### Study area

The Parana River is the largest sub basin of the La Plata River Basin located in South America, covering part of Argentina, Brazil, Paraguay. Draining great part of the central south South America. The reservoir of Itaipu connected two distinct freshwater ecoregions of the world: Upper and Lower Parana Ecoregions (Abell *et al.* 2008), because when Itaipu was completed it eliminated Sete Quedas falls (Map on previous chapter also presented in Vitule *et al.* 2012b), an important vicariant barrier and an ecological filter for freshwater fish faunas (Bonetto 1986) allowing the freshwater fish fauna of Lower Paraná to ascend through Upper Parana Region.

### Freshwater fish species list

The species base list for the studied region was obtained from (Vitule *et al.* 2012b), the list was actualized and modified when: There were discrepancies between the authors on the original list about origin of some species, if they were native to the upper or native to the lower ecoregion, we used Graça and Pavanelli book (2007) to decide. The species that couldn't be solved this way were considered potential invader if any author of the original list said so. Taxonomic validity of all species was checked against Fishbase database (Froese and Pauly 2012). Since our interest is mainly on the lower region native species that had the chance to colonize, species that were translocated from other countries/basins or that were added through aquaculture, sport-fishing, live-bait or aquarium trades were excluded from the database. The list contains the taxonomic status and the following most common available functional traits: From Fishbase database (Froese and Pauly 2012), we retrieved maximum recorded body length (cm), log transformed to fit a normal distribution, and trophic level. Reproductive strategies for each species were retrieved from Fishbase and Check List of the Freshwater Fishes of South and Central America (Reis *et al.* 2003), while other solved with expert ichthyologists. The reproductive strategies were categorized based on the classification present in Agostinho *et al.* (2004). A functional approach is relevant to use for freshwater fishes, as attributes like life history traits have been used with efficacy to be predictors of fish strategies in relation to the environment they use (Mims *et al.* 2010, Mims and Olden 2013) and to predict invasions (e.g., Kolar and Lodge 2002, Vila-

Gispert *et al.* 2005, Olden *et al.* 2006). To test Darwin's hypotheses, we explicitly assume that all species present and natural of the lower ecoregion would have sufficient time to be mobile enough to have the opportunity to disperse, and to colonize the upper region after the impoundment of the biogeographic barrier. All species from lower region that after 25 years are presently captured in Upper region were assumed to be established.

## Statistical Analysis

**Taxonomically:** Species that had the opportunity to colonize were plotted in a 2x2 contingency tables. Divided into species that have a congeneric native and those without, and species that established and those that do not. Table was separated into following monophyletic groups, Siluriformes and Characiformes while other orders were grouped together as they had not enough *n* on every subgroup to fit the criteria for Fisher's exact test. A failure % was calculated as the proportion of failed per total of species that had the opportunity to colonized belonging to that taxonomic group, as a descriptive statistics to see any trend. A one-tailed Fisher Exact Test was used to examine the independence of row and column data for the orders and all species as they contain enough *n*. To determine if successful invaders are more likely than failed invaders to belong to unshared genera. Left-tail significance would favor naturalization and right-tail significance would favor pre-adaptation hypotheses. Statistical tests were conducted on the built-in commands inside the R language, no additional packages required (R Development Core Team 2012).

**Alpha niche through functional traits:** Functional traits are said to better capture resource use of species allowing the comparisons between species to be more realistic, indicating with more fidelity a possible competition and biotic resistance (Kunstler *et al.* 2012). A functional trait matrix containing, maximum recorded body length (cm) log transformed, trophic level and reproductive strategy were transformed into a distance matrix using Gower's distance for every successful and failed species. Gower's distance index support mixed variables, continuous, ordinal and categorical; there were no hierarchy assumption on categorical variable (Gower 1971), present on 'cluster' package of R software (Maechler *et al.* 2012). From this distance matrix we computed two distance metrics outlined by Thuiller *et al.* (2010)

to quantify invaders relatedness to the assemblage: 'Distance of the invader to its Nearest Native Species in the native assemblage (DNNS)' and 'Mean Distance of the invader relative to Native Species (MDNS)' as we lack abundance data we haven't tested other proposed metrics. DNNS metrics assumes that biotic resistance imposed by native assemblage is driven by its most functionally similar. MDNS assumes a equal contribution of entire native assemblage to overall biotic resistance. Mann – Whitney U test was used to verify if there was difference in the distributions between the group that had success and the group that failed, in the above mentioned metrics. Non-parametric test was chosen due to samples not have equivalent  $n$  and data isn't normally distributed. Programming was conducted on R language, statistical tests were conducted using the built-in commands inside the R software, no additional package were required (R Development Core Team 2012).

### **Conceptual model**

Functional niche similarity between each potential invaders and native species can be described by three mathematical models concerning similarity distances of each native species to each potential invader. First, successful or 'failed invaders' (i.e. nonnatives introduced species that failed along the invasive process) can be similar to most native species. Therefore, invasion success could be explained by the fact that the habitat is suitable for invaders and; invasion failure is probably due to competition among similar native species (Lockwood *et al.* 2007). In this case, an exponential model will describe the pattern of similarity between a certain invader and native species (Line I in figure 1). Alternatively, successful or failed invaders can be dissimilar to most native species. Invasion success may be explained by resource availability and/or the lack of competitors (Lockwood *et al.* 2007), spatial heterogeneity (Davies *et al.* 2005) and invasion failure can be explained by the lack of resource availability, for example lack of microhabitat or proper environmental condition (Wiens and Graham 2005). It also could be due to neutral mechanism of dispersal (Hubbel 2001) and the impossibility to quantify niche and its possible compartmentalization with precision using those functional traits (Gosselin 2012, Kunstler *et al.* 2012). In this case, a logarithmic model will describe the pattern of similarity between a potential invader and native species (Line II in Figure 1). Another possibility can be observed if the pattern of similarity between a certain invader and native species is linear (Line III in Figure 1). In other words, invader is

similar and dissimilar to the same proportion of native species. In this case, invasion success and failure are probably explained by other reasons than resource availability and competition with native species, like dispersal assembly of neutral theory (Hubbel 2001). The three conceptual models are summarized in Figure 1.

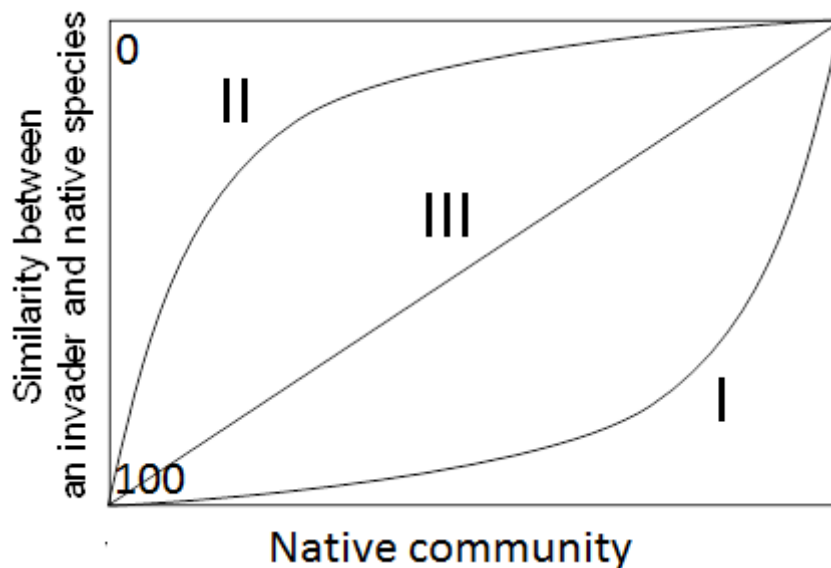


Figure 1. Possible patterns of similarity between an invader and native species. In pattern I, invasion success is probably due to resource availability and/or absence of competition; and invasion failure due to the probability of finding competition. In pattern II, invasion success is probably due to low probability of competition; and invasion failure due to resource suitability. In pattern III, invasion success and fail may be due to other mechanisms (e.g. propagule pressure, neutral mechanism in our scale).

#### *Data analysis of conceptual model*

Potential invaders were divided into group that had success and group that failed to establish, same procedure of 'alpha niche' to calculate distance matrix was used, but instead of grouping them together we used all the distances between each invader and all the native assemblage. The distance valued of each invader was fitted to linear, exponential and logarithmic curves through a non-linear regression with brute force command from 'nls2' package in R (Grothendieck 2010). The best fitted curve, measured through Akaike's information criterion (Sakamoto *et al.* 1986), was selected, resulting in a table of frequencies for each curve for both groups, Chi-square was used to verify if the proportion of the models were the same between both groups. Statistics and programming were compiled on R language (R Development Core Team 2012).

## Results

The 213 species, 33 families and 116 genera, had the opportunity to colonize. 54 were successful and 159 failed to colonize the Upper stretches of Paraná. Fisher's exact test (table 1) shown that ratio of unshared/shared genera on successful and failed invaders were the same. The left tail tests were almost significant for Characiformes ( $p = 0.07$ ), what would suggest the naturalization hypothesis.

Table 1. Numbers of introduced fish species belonging to shared and unshared genera by native species. Orders are in bold, family underlined and genera are in normal text and belong to the family right over it. Failure % is the proportion of failed per total of species that had the opportunity to colonized belonging to that taxonomic group.

	Successful invaders		Failed invaders		% Failure	p - value	
	Shared	Unshared	Shared	Unshared		Left tail	Right tail
<b>Siluriformes</b>	<b>12</b>	<b>11</b>	<b>33</b>	<b>31</b>		<b>0.615</b>	<b>0.576</b>
<u>Asprenidae</u>	0	0	1	5	100.0		
<u>Auchnipteridae</u>	3	0	2	0	40.0		
<u>Callichthyidae</u>	0	1	5	0	83.3		
Corydoras	0	0	5	0	100.0		
<u>Doradidae</u>	0	5	0	3	37.5		
<u>Heptapteridae</u>	2	0	3	0	60.0		
<u>Loricariidae</u>	6	3	14	14	75.7		
Hypostomus	5	0	6	0	54.5		
Loricariichtys	0	2	0	3	60.0		
Otocinclos	0	0	0	4	100.0		
<u>Pimelodidae</u>	1	2	5	7	80.0		
Pimelodus	1	0	5	0	83.3		
<u>Pseudopimelodidae</u>	0	0	1	0	100.0		
<u>Trychomycteridae</u>	0	0	2	2	100.0		
<b>Characiformes</b>	<b>8</b>	<b>9</b>	<b>40</b>	<b>17</b>		<b>0.073</b>	<b>0.978</b>
<u>Acestrorhynchidae</u>	1	0	0	0	0.0		
<u>Anostomidae</u>	1	0	3	1	80.0		
<u>Characidae</u>	3	6	29	10	81.3		
Astyanax	0	0	8	0	100.0		
Bryconamericus	1	0	4	0	80.0		
Hyphessobrycon	0	0	6	0	100.0		
Oligosarcus	0	0	3	0	100.0		
<u>Crenuchidae</u>	1	0	3	0	75.0		
Characidium	1	0	3	0	75.0		
<u>Curimatidae</u>	2	0	5	3	88.9		
Cyphocharax	1	0	3	0	75.0		
<u>Erythrinidae</u>	0	2	0	0	0.0		

<u>Gasteropelecidae</u>	0	0	0	1	100.0		
<u>Hemiodontidae</u>	0	1	0	1	50.0		
<u>Pristigasteridae</u>	0	0	0	1	100.0		
<b>Other groups</b>	<b>6</b>	<b>8</b>	<b>14</b>	<b>24</b>	73.1	<b>0.765</b>	<b>0.466</b>
<u>Achiridae</u>	0	1	0	0	0.0		
<u>Anablepidae</u>	0	0	0	1	100.0		
<u>Apteronotidae</u>	3	0	0	0	0.0		
<u>Atherinopsidae</u>	0	1	0	0	0.0		
<u>Belonidae</u>	0	0	0	2	100.0		
<u>Cichlidae</u>	0	0	10	9	100.0		
Apistograma	0	0	0	4	100.0		
Crenicichla	0	0	4	0	100.0		
Gymnogeophagus	0	0	3	0	100.0		
<u>Clupeidae</u>	0	0	0	1	100.0		
<u>Gymnotidae</u>	3	0	0	0	0.0		
<u>Hypopomidae</u>	0	1	0	1	50.0		
<u>Lepidosirenidae</u>	0	0	0	1	100.0		
<u>Poeciliidae</u>	0	0	3	0	100.0		
<u>Potamotrygonidae</u>	0	2	0	4	66.7		
<u>Rhamphichthyidae</u>	0	2	0	0	0.0		
<u>Rivulidae</u>	0	0	0	3	100.0		
<u>Sciaenidae</u>	0	0	0	2	100.0		
<b>All Species</b>	<b>26</b>	<b>28</b>	<b>87</b>	<b>72</b>		<b>0.289</b>	<b>0.809</b>



## Alpha niche

Mann-Whitney of MDNS metric showed that there was no difference in distribution of the success and failed groups ( $W = 3991.5$ ,  $p = 0.52$ ) (Fig 2). The DNNS was significant ( $W = 3816$ ,  $p = 0.27$ ), success was more dissimilar with nearest native species than failed; distributions are shown in a Kernel density plot (Figure 2).

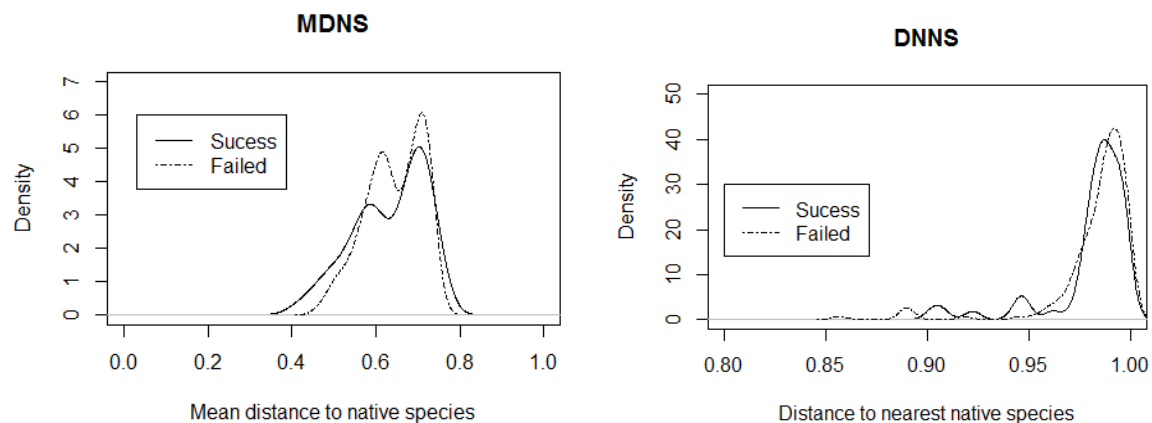


Figure 2: Kernel density plot of data distribution of Gower's similarity index of MDSN – Mean Distance to Native Species and DNNS – Distance to Nearest Native Species.

## Conceptual approach

For successful and failed invaders all the hypothesized curves were present, linear models were more frequently select than non-linear models (logarithmic and exponential) for both groups (Figure 3). There was no significant difference in the proportion of selected models between the groups ( $\chi^2 = 4.204$ , d.f. = 2,  $p > 0.12$ ).

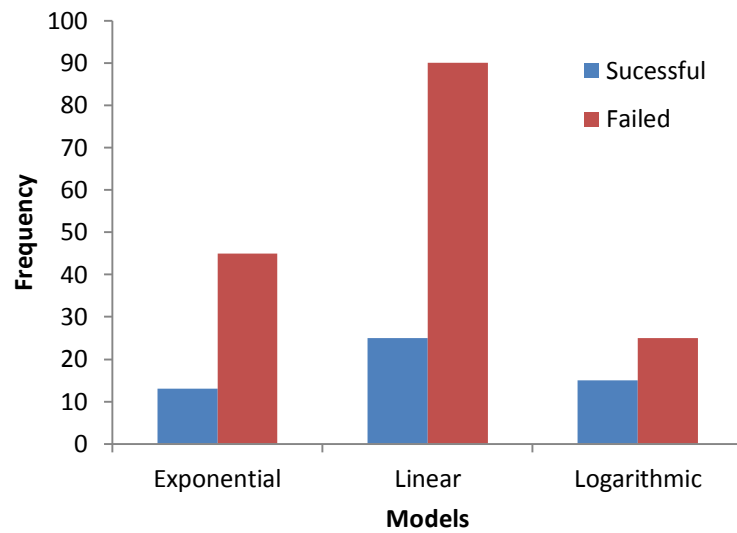


Figure 3: Frequencies of the three conceptual models selections of Failed ( $n = 160$ ) and Successful ( $n = 53$ ) potential invaders subgroups through Akaike's criterion.

## Discussion

Darwin's original hypothesis (1859) implicates that species would have to interact with each other to produce the outcome expected for coexisting patterns. At this coarse scale can't be assumed species interactions to be happening and driving the totality of its patterns. As spatial scale increases direct interactions between species become less important and taxonomic patterns might change dramatically (Proches *et al.* 2008, Thuiller *et al.* 2010). The large scale might be a potential source of criticism but rather than simple estimating or sometimes using only species that had success or become naturalized and mainly underestimating failed invaders, we are sure of the sympatric donor pool that is restricted to the aquatic environment. The large area mixed together with the reservoir deals with the problem of 'propagule pressure' as possibly entire populations were captured in the area, netting enough individual numbers to keep a reproducing population in the novel area to become naturalized (Lockwood *et al.* 2009), those that do not established could be because they were absent on the capture event or they would have never reached the capture area by other mechanism. Also using functional traits to quantify niche we go beyond the assumption of that taxonomy might reflects ecological resemblance what seems acknowledge error (Ricciardi and Mottiar, 2006, Thuiller *et al.* 2010).

Taxonomically evaluations of Darwin's hypothesis did not support naturalization nor pre adaptation hypothesis, it makes broader assumptions like that all species in each genus are evenly related, every congener compete with the same strength, making biotic resistance being as a factor of how much congeners exist (Ricciardi and Attkinson 2006). However, genera may differ in speciation times, meaning that species in different genera will be related to varying degrees. Even if genera are monophyletic they still often vary considerably between specialists and generalists (Humphreys and Linder 2009) and may present different life history strategies, considerably varying from opportunistic to equilibrium strategies (Mims *et al.* 2010). Being on same genera doesn't necessarily means they will directly compete with each other than they would compete with a more functional related species in the native assemblage. Characiformes trend could be interpreted as a

confirmation of Darwin, but further investigations on reduced scale must be made. A possible explanation is that a Characiformes might use more lentic systems, that are absent in reservoirs, while Siluriformes are better adapted to lotic systems. Meaning Characiformes would have a higher amount of failed invaders in comparison to Siluriformes, if we ponder both by their natural diversity and chance of having congeners on native counterpart, as they are most diverse groups on Neotropics (Castro 1999). When taxonomic table is refined we see that some taxonomic groups had a complete failure like genus *Astyanax*, *Corydoras*, entire Cichlidae family. A possibility to be considered to explain those failures is that even considering high species mobility, some taxonomic groups are still restricted to some areas, like headwaters. Also, species might be under effect of neutral or random mechanism considering dispersal (Hubbel 2001) or being filtered by competition or niche suitability in their respective sub-system (small rivers, headwaters). Those impediments would not let species reach the reservoir capture area.

The 'alpha niche' approach through functional traits shown that overall biotic resistance (accounted in MDNS) show no trend to Darwin's hypothesis, it can be related on the fact that on this richness, spatial scale and number of functional traits analyzed, we'd expect a few species to be really similar and few very dissimilar, with a high number of species being account on average similarity. Carboni *et al.* (2012) also reached the same conclusion that this metrics of mean assemblage relatedness seems unclear and uninformative, as invaders had large confidence intervals, that overlap with intervals of natives, what was shown in density plots (Figure 2). All this make an ideal call for how animal ecologist view functional traits, as mentioned by Gosselin (2012) the use of a mean specialization index isn't leading to an important contribution to understanding species success or extirpations. This brings the importance of the natural history, autoecology and other basic ecological works and species descriptions. Basic knowledge plays a key role in allowing researchers to understand and better partition functional traits that represent response and actions on the system (Lockwood *et al.* 2007, Gosselin 2012, Strayer 2012). Basic works also prove useful to provide the ability to ordinate traits in a scale of competitiveness as it's already being made with plants (Kunstler *et al.* 2012) could show better result on explaining the variation in establishment success. Resistance imposed by the nearest native in terms of functional traits (accounted in DNNS), shown a trend, even

though not statically significant, that could be interpreted favoring Darwin. Success seems to be more dissimilar to native species than failed group. As we cannot really show that biotic interactions are occurring/driving the selection on the scale, because invaders could colonize and establish the novel environment without ever encountering a similar native that would compete. The success of more dissimilar species may be the result of potential 'empty niche' occupancy by non-natives containing slightly different set of traits while meeting the environmental requirements to establish there (Shea and Chesson 2002). If we do accept some degree of competition, the result might be a reflection that biotic resistance of the native area is driven by the most functional/ecological similar native species present. As pointed by Kraft *et al.* (2007), one single strong competitor is enough to competitively exclude a potential invader; even though competition measures weren't assessed. And lastly, the trend might be a reflection that nearest distance to a native species metrics might be capturing other species that are similar in functional traits to the native being compared, and the biotic resistance is being driven by more than a single species. A question that would be interesting to be addressed in future opportunities.

The conceptual model seems to be the most realistic when comparing each invader against every native species as it compares then individually instead of a mean index of functionality of native assemblage (Gosselin 2012). It might play an important role in understanding effects on small scales with lower diversity. The high number of combinations of functional traits that generate a high number of similar intermediate values, it is what probably drawn many of species to a linear model on the conceptual model. But it's interesting that on both group of potential invaders the logarithmic and exponential curves were selected. Giving us a hint that mechanism that select based on how similar or how dissimilar an invader might be in action. This conceptual model has its flaws, as if we increase richness even more or add more functional traits it will probabilistic selects linear models more than any other. This may be improved if we take action on trait hierarchy suggestion above (Kunstler *et al.* 2012), and greatly improve using smaller spatial scale, as it has smaller diversity and this lead to the ability to retrieve better data about other functional traits and abundance and relate it to where competition matters (Carboni *et al.* 2012).

Moyle and Light (1996b) said that for freshwater fish fauna biotic resistance is of minor importance and given proper environmental conditions, time and colonization opportunity exotic species will invade independent of the native assemblage. While our results seem to go on this way, we believe that the scale used is the most influential settings to our results. Because scale is recognized to influence on the out coming result of the tests in patterns of similarity between exotics and natives, consistent with Darwin's Conundrum (Diez *et al.* 2008; Proches *et al.* 2008; Thuiller *et al.* 2010). What we may have seen is niche suitability and lack of invasion mobility and not competition. As we cannot really predict biotic interaction between the species in the scale used, invader species could spread across the environment without the need to enter in competing state or would fail due to not encountering suitable habitats for its life cycle. As next step, reducing the spatial scale used we could confirm Darwin's naturalization hypothesis *per se*, because it's where biotic interactions are expected to be important and to occur.

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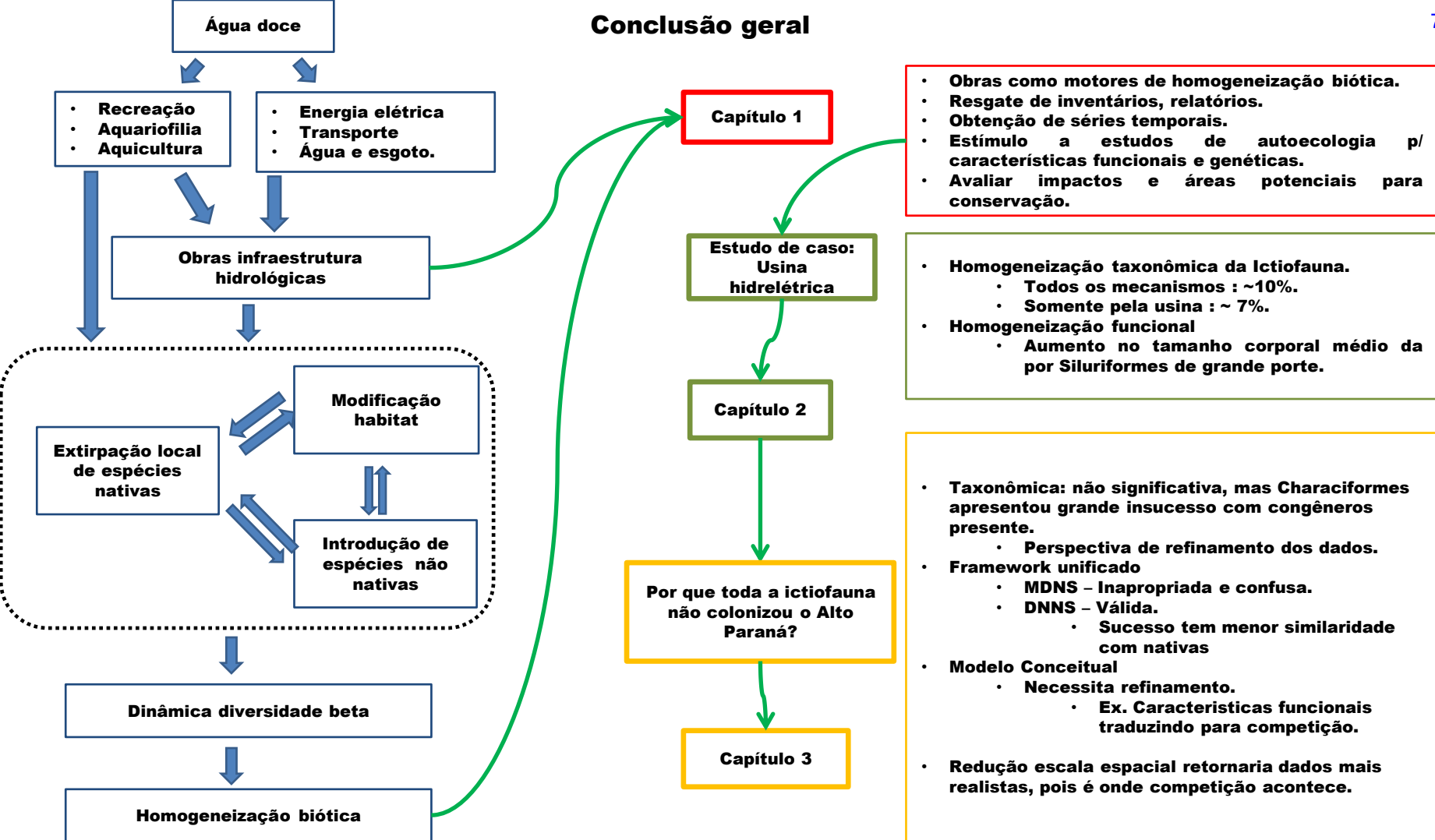
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## Conclusão geral



**Fluxograma conclusão geral:** O uso de relatórios e outros inventários gerados pelas obras de infraestruturas podem contribuir para o entendimento destas como geradores do processo de homogeneização biótica. Outro fator decisivo para explorar o assunto com as obras é obtenção de séries temporais, tão necessárias para elucidar as dinâmicas do processo. O estudo de caso, mostrou que a homogeneização biótica da ictiofauna causada pela usina correspondeu a mais de 50% da homogeneização por todos os mecanismos (aquicultura, aquariorfilia, pesca esportiva). Isso mostra a relevância de considerar a perda de diversidade beta ao projetar obras e selecionar locais a serem preservados, bem como avaliar estratégias para transposição, restauração e regulação de águas. No estudo de caso nos deparamos com variabilidade no sucesso de colonização das espécies após a construção de reservatórios. Utilizando a hipótese de naturalização Darwin, não fomos capazes de confirmar definitivamente que a presença de gêneros correlatos influenciam no sucesso. Considerando o efeito da escala, o resultado obtidos para Characiformes pode ser sim um efeito relacionado a presença de congêneros, que certamente vale a pena ser aprofundando. A métrica distância a espécie nativa mais funcionalmente parecida, também corroborou a hipótese de Darwin, mas pela escala é difícil atribuir a um efeito de competição. Um refinamento da escala espacial e como as características funcionais refletem uso do nicho seriam um próximo passo para abordar a hipótese.

## APENDICES

### APPENDIX 1 CHAPTER 2

List of fish species presence-absence data in the aquatic ecoregions of Lower and Upper Paraná River before and after fish introductions. Lower Paraná before total introduction  
 Paraná before introductions (*sensu* Júlio Jr. et al., 2009) - **UBIJ**; Upper Paraná before introductions (*sensu* Langeani *et al.*, 2007) - **UBIL**; Upper Paraná after total introduction  
 2007) - **UAIL**; Upper Paraná after Itaipú dam (*sensu* Júlio Jr. et al., 2009) - **UAIJ**. **Status** - threatened and/or rare. **Size** - maximum body length (cm). **Tactic** - short/long distance  
 and trophic level of species follows FishBase (Froese & Pauly, 2011).

Species	LBTI	LATI	UBIJ	UBIL	UATI	UAIL	UAIJ	status	Trophic level	Size	Tactic	introduction
<i>Abramites hypselonotus</i>	1	1	0	0	0	0	0		2.93	14	Non-migrant	
<i>Acestrorhynchus lacustris</i>	0	0	1	1	1	1	1		4.2	27	Non-migrant	
<i>Acestrorhynchus pantaneiro</i>	1	1	0	0	1	0	0		4.23	35.2	Non-migrant	piracema channel
<i>Aequidens plagiozonatus</i>	1	1	0	0	0	0	0		3.19	10.3	Non-migrant	
<i>Ageneiosus inermis</i>	1	1	0	0	1	1	1		3.98	59	Non-migrant	Itaipú dam
<i>Ageneiosus militaris</i>	1	1	1	0	1	1	1		3.76	30	Non-migrant	Itaipú dam
<i>Ageneiosus ucayalensis</i>	1	1	0	1	1	1	1		3.66	29	Non-migrant	Itaipú dam
<i>Amaralia cf. hypsiura</i>	1	1	0	0	0	0	0		3.17	13.3	Non-migrant	
<i>Anadoras weddellii</i>	1	1	0	0	0	0	0	Argentina	2.81	15	Non-migrant	
<i>Ancistrus cirrhosus</i>	1	1	1	1	1	1	1		2	8.9	Non-migrant	
<i>Ancistrus dubius</i>	1	1	0	0	0	0	0		2	12.6	Non-migrant	
<i>Ancistrus piriformis</i>	1	1	0	0	0	0	0		2.16	8.3	Non-migrant	
<i>Apareiodon affinis</i>	1	1	1	1	1	1	1		2.21	14.3	Non-migrant	
<i>Apareiodon ibitiensis</i>	0	0	1	1	1	1	1		2.3	11.3	Non-migrant	
<i>Apareiodon piracicabae</i>	0	0	1	1	1	1	1		2.28	12	Non-migrant	
<i>Apareiodon vladii</i>	0	0	1	1	1	1	1		2.3	11.3	Non-migrant	
<i>Aphyocharax anisitsi</i>	1	1	1	0	1	1	1		3.22	5.5	Non-migrant	Itaipú dam
<i>Aphyocharax dentatus</i>	1	1	1	1	1	1	1	Argentina	3.02	7.2	Non-migrant	
<i>Aphyocheirodon hemigrammus</i>	0	0	1	1	1	1	1		2.51	4.8	Non-migrant	
<i>Apistogramma borellii</i>	1	1	0	0	0	0	0		3.26	3.9	Non-migrant	
<i>Apistogramma commbrae</i>	1	1	0	0	0	0	0		3.17	3.3	Non-migrant	
<i>Apistogramma inconspicua</i>	1	1	0	0	0	0	0		3.29	3.8	Non-migrant	
<i>Apistogramma trifasciata</i>	1	1	0	0	0	0	0		3.29	3.8	Non-migrant	
<i>Apteronotus albifrons</i>	1	1	1	0	1	1	1		3.03	50	Non-migrant	Itaipú dam
<i>Apteronotus brasiliensis</i>	0	0	0	0	1	0	0		3.31	29	Non-migrant	unknown
<i>Apteronotus caudimaculosus</i>	1	1	0	0	1	1	1		3.31	28.7	Non-migrant	Itaipú dam
<i>Apteronotus ellisi</i>	1	1	1	0	1	1	1		3.32	32.8	Non-migrant	Itaipú dam

<i>Aristichthys nobilis</i>	0	1	0	0	1	0	0		2.33	146	Non-migrant	fish-farming
<i>Aspidoras fuscoguttatus</i>	0	0	1	1	1	1	1		2.97	3.8	Non-migrant	
<i>Aspidoras lakoi</i>	0	0	1	1	1	1	1		2.97	4	Non-migrant	
<i>Astronotus crassipinnis</i>	1	1	0	0	1	1	1		3.03	24	Non-migrant	Itaipú dam
<i>Astyanax abramis</i>	1	1	0	0	0	0	0		2.76	14	Non-migrant	
<i>Astyanax altiparanae</i>	0	0	1	1	1	1	1		2.84	10.6	Non-migrant	
<i>Astyanax asuncionensis</i>	1	1	0	0	0	0	0		2.83	15	Non-migrant	
<i>Astyanax bimaculatus</i>	1	1	0	0	0	0	0		2.17	17.5	Non-migrant	
<i>Astyanax biotae</i>	0	0	1	1	1	1	1		2.8	9	Non-migrant	
<i>Astyanax bockmanni</i>	0	0	1	1	1	1	1		2.8	9	Non-migrant	
<i>Astyanax correntinus</i>	1	1	0	0	0	0	0		2.8	9	Non-migrant	
<i>Astyanax eigenmanniorum</i>	1	1	1	1	1	1	1		2.86	4.9	Non-migrant	
<i>Astyanax fasciatus</i>	1	1	1	1	1	1	1		2.75	16.8	Non-migrant	
<i>Astyanax goyacensis</i>	0	0	1	1	1	1	1		2.8	9	Non-migrant	
<i>Astyanax leonidas</i>	1	1	0	0	0	0	0		2.87	4.6	Non-migrant	
<i>Astyanax paranae</i>	0	0	1	1	1	1	1		2.8	11.3	Non-migrant	
<i>Astyanax paranahybae</i>	0	0	1	1	1	1	1		2.8	9	Non-migrant	
<i>Astyanax scabripinnis</i>	1	1	0	0	0	0	0		2.88	7.8	Non-migrant	
<i>Astyanax schubarti</i>	0	0	1	1	1	1	1		3.14	9	Non-migrant	
<i>Astyanax trierythropterus</i>	0	0	1	1	1	1	1		2.8	9	Non-migrant	
<i>Astyanax troya</i>	1	1	0	0	0	0	0		2.81	7.4	Non-migrant	
<i>Astyanax tupi</i>	1	1	0	0	0	0	0		2.81	7.3	Non-migrant	
<i>Auchenipterus nigripinnis</i>	1	1	0	0	0	0	0		3.57	20.2	Non-migrant	
<i>Auchenipterus osteomystax</i>	1	1	0	1	1	1	1		3.6	27	Non-migrant	Itaipú dam
<i>Australoheros facetus</i>	1	1	1	1	1	1	1		3.33	19.3	Non-migrant	
<i>Australoheros guarani</i>	1	1	0	0	0	0	0		3.18	12.9	Non-migrant	
<i>Austrolebias bellottii</i>	1	1	0	0	0	0	0		3.26	7	Non-migrant	
<i>Austrolebias nigripinnis</i>	1	1	0	0	0	0	0		3.12	7	Non-migrant	
<i>Austrolebias paranaensis</i>	1	1	0	0	0	0	0		3.16	7	Non-migrant	
<i>Bergiaría platana</i>	1	1	0	0	0	0	0		3.57	9.1	Non-migrant	
<i>Bergiaría westermanni</i>	1	1	0	0	0	0	0		3.57	9.1	Non-migrant	
<i>Brachyhypopomus brevirostris</i>	1	1	0	0	0	0	0		3.2	34.7	Non-migrant	
<i>Brachyhypopomus gauderio</i>	1	1	0	0	1	0	1		3	14.9	Non-migrant	fish bait / Itaipú dam
<i>Brycon hilarii</i>	0	0	0	0	1	0	0		2	56	Migratory	unknown
<i>Brycon nattereri</i>	0	0	1	1	1	1	1	Brazil	2.62	29	Migratory	
<i>Brycon orbignyanus</i>	1	1	1	1	1	1	1	Brazil	2.51	79	Migratory	
<i>Bryconamericus agna</i>	1	1	0	0	0	0	0		2.64	6.5	Non-migrant	
<i>Bryconamericus eigenmanni</i>	1	1	0	0	0	0	0		2.66	6.1	Non-migrant	
<i>Bryconamericus exodon</i>	1	1	0	0	1	1	0		2.73	5.7	Non-migrant	unknown / piracema channel

<i>Bryconamericus iheringii</i>	1	1	1	1	1	1	1	Argentina	2	11	Non-migrant	
<i>Bryconamericus mennii</i>	1	1	0	0	0	0	0		2.69	11.4	Non-migrant	
<i>Bryconamericus rubropictus</i>	1	1	0	0	0	0	0		2.66	11.4	Non-migrant	
<i>Bryconamericus stramineus</i>	1	1	1	1	1	1	1		2.73	11.4	Non-migrant	
<i>Bryconamericus turiuba</i>	0	0	1	1	1	1	1		2.66	6.1	Non-migrant	
<i>Bujurquina vittata</i>	1	1	0	0	0	0	0		3.38	9	Non-migrant	
<i>Bunocephalus doriae</i>	1	1	0	0	0	0	0		3.13	8.3	Non-migrant	
<i>Bunocephalus larai</i>	0	0	1	1	1	1	1		3.09	5	Non-migrant	
<i>Callichthys callichthys</i>	1	1	1	1	1	1	1		2.95	17	Non-migrant	
<i>Catathyridium jenynsii</i>	1	1	0	0	1	1	1		3.31	23	Non-migrant	Itaipú dam
<i>Cetopsis gobioides</i>	1	1	1	1	1	1	1	Argentina	3.64	10.9	Non-migrant	
<i>Cetopsorhamdia iheringi</i>	0	0	1	1	1	1	1		2.98	10.6	Non-migrant	
<i>Chaetobranchopsis australis</i>	1	1	0	0	0	0	0		3.5	12	Non-migrant	
<i>Characidium etzeli</i>	1	1	0	0	0	0	0		3.09	5.6	Non-migrant	
<i>Characidium fasciatum</i>	0	0	1	1	1	1	1		2.89	6.7	Non-migrant	
<i>Characidium gomesi</i>	0	0	1	1	1	1	1		3.1	6.5	Non-migrant	
<i>Characidium heirmostigmata</i>	0	0	1	1	1	1	1		3.09	5.4	Non-migrant	
<i>Characidium laterale</i>	1	1	0	0	1	1	0		3.1	3.5	Non-migrant	Itaipú dam
<i>Characidium occidentale</i>	1	1	0	0	0	0	0		3.08	4.8	Non-migrant	
<i>Characidium oiticicai</i>	0	0	1	1	1	1	1		3.1	6.8	Non-migrant	
<i>Characidium rachovii</i>	1	1	0	0	0	0	0		3.07	4.3	Non-migrant	
<i>Characidium schubarti</i>	0	0	1	1	1	1	1		3.25	51.3	Non-migrant	
<i>Characidium xanthopterygion</i>	0	0	1	1	1	1	1		3.08	4.7	Non-migrant	
<i>Characidium zebra</i>	1	1	1	1	1	1	1		3.2	6.5	Non-migrant	
<i>Charax leticiae</i>	1	1	0	0	0	0	0		3.7	10	Non-migrant	
<i>Chasmocranus brachynema</i>	0	0	1	1	1	1	1		3.32	13.1	Non-migrant	
<i>Cheirodon interruptus</i>	1	1	0	0	0	0	0	Argentina	2.39	5.8	Non-migrant	
<i>Cichla kelberi</i>	0	0	0	0	1	0	0		4.08	27.6	Non-migrant	angling / fish stocking
<i>Cichla piquiti</i>	0	0	0	0	1	0	0		4.25	43	Non-migrant	angling / fish stocking
<i>Cichlasoma dimerus</i>	1	1	0	0	0	0	0		3.44	11.7	Non-migrant	
<i>Cichlasoma paranaense</i>	0	0	1	1	1	1	1		3.33	7.4	Non-migrant	
<i>Cichlasoma pusillum</i>	1	1	0	0	0	0	0		3.31	6.6	Non-migrant	
<i>Clarias gariepinus</i>	0	1	0	0	1	0	0		3.15	170	Non-migrant	fish-farming
<i>Clupeacharax anchoveoides</i>	1	1	0	0	0	0	0		3.02	6.6	Non-migrant	
<i>Cnesterodon hypselurus</i>	0	0	1	1	1	1	1		2.97	3.1	Non-migrant	
<i>Cnesterodon raddai</i>	1	1	0	0	0	0	0		2.98	2.3	Non-migrant	
<i>Colossoma macropomum</i>	0	0	0	0	1	0	0		2.02	108	Non-migrant	fish-farming
<i>Coptobrycon bilineatus</i>	0	0	1	1	1	1	1	Brazil	3	4.1	Non-migrant	
<i>Corumbataia britskii</i>	0	0	1	1	1	1	1		2	2.7	Non-migrant	

<i>Corumbataia cuestae</i>	0	0	1	1	1	1	1		2.25	3.3	Non-migrant	
<i>Corydoras aeneus</i>	1	1	1	1	1	1	1		2.96	7.5	Non-migrant	
<i>Corydoras diffluvialilis</i>	0	0	1	1	1	1	1		2.95	4.7	Non-migrant	
<i>Corydoras diphys</i>	1	1	0	0	0	0	0		2.95	4.5	Non-migrant	
<i>Corydoras ehrhardti</i>	0	0	1	1	1	1	1		3.2	4.1	Non-migrant	
<i>Corydoras ellisae</i>	1	1	0	0	0	0	0		2.95	5	Non-migrant	
<i>Corydoras flaveolus</i>	0	0	1	1	1	1	1		2.97	3.4	Non-migrant	
<i>Corydoras hastatus</i>	1	1	0	0	0	0	0		2.98	2.4	Non-migrant	
<i>Corydoras micracanthus</i>	1	1	0	0	0	0	0		2.96	4	Non-migrant	
<i>Corydoras nattereri</i>	0	0	1	1	1	1	1		2.94	5.4	Non-migrant	
<i>Corydoras paleatus</i>	1	1	1	1	1	1	1		2.94	5.9	Non-migrant	
<i>Corydoras undulatus</i>	1	1	0	0	0	0	0		2.95	4.4	Non-migrant	
<i>Creagrutus varii</i>	0	0	1	1	1	1	1		2.57	4.2	Non-migrant	
<i>Crenicichla britskii</i>	0	0	1	1	1	1	1		3.14	4.5	Non-migrant	
<i>Crenicichla haroldoi</i>	0	0	1	1	1	1	1		3.16	9.8	Non-migrant	
<i>Crenicichla jaguarensis</i>	0	0	1	1	1	1	1		3.19	14.8	Non-migrant	
<i>Crenicichla jupiaensis</i>	0	0	1	1	1	1	1	Brazil	3.14	8.2	Non-migrant	
<i>Crenicichla lepidota</i>	1	1	0	0	0	0	0		3.56	18	Non-migrant	
<i>Crenicichla mandelburgeri</i>	1	1	0	0	0	0	0		3.17	11.5	Non-migrant	
<i>Crenicichla niederleini</i>	1	1	1	1	1	1	1		3.23	23.5	Non-migrant	unknown
<i>Crenicichla semifasciata</i>	1	1	0	0	0	0	0		3.2	15	Non-migrant	
<i>Crenicichla vittata</i>	1	1	0	0	0	0	0		3.24	26	Non-migrant	
<i>Curimatella dorsalis</i>	1	1	0	0	0	0	0		2.15	11.4	Non-migrant	
<i>Cynopotamus argenteus</i>	1	1	0	0	0	0	0		3.95	24	Non-migrant	
<i>Cynopotamus kincaidi</i>	1	1	0	0	1	1	0		3.95	25.8	Non-migrant	Itaipú dam
<i>Cyphocharax gillii</i>	1	1	0	0	1	1	0		2	10	Non-migrant	Itaipú dam
<i>Cyphocharax modestus</i>	1	1	1	1	1	1	1		2	16.2	Non-migrant	
<i>Cyphocharax nagelii</i>	0	0	1	1	1	1	1		2	16.3	Non-migrant	
<i>Cyphocharax platanus</i>	1	1	0	0	0	0	0		2	13.4	Non-migrant	
<i>Cyphocharax spilatus</i>	1	1	0	0	0	0	0		2.08	8.9	Non-migrant	
<i>Cyphocharax vanderi</i>	0	0	1	1	1	1	1		2.23	6.8	Non-migrant	
<i>Cyphocharax voga</i>	1	1	0	0	0	0	0		2	19.6	Non-migrant	
<i>Cyprinus carpio</i>	0	1	0	0	1	0	0		2.96	110	Non-migrant	fish-farming
<i>Diapoma terofali</i>	1	1	0	0	0	0	0	Argentina	3.24	4.8	Non-migrant	
<i>Doras eigenmanni</i>	1	1	0	0	1	1	1	Argentina	2.83	10	Non-migrant	Itaipú dam
<i>Eigenmannia trilineata</i>	1	1	1	1	1	1	1		3.05	25	Non-migrant	
<i>Eigenmannia virescens</i>	1	1	1	1	1	1	1		3	35.8	Non-migrant	
<i>Erythrinus erythrinus</i>	1	1	0	0	1	0	0		3.73	20	Non-migrant	fishing / fish bait / Itaipú dam
<i>Farlowella hahni</i>	1	1	0	0	1	1	0		2.34	20.1	Non-migrant	Itaipú dam

<i>Farlowella oxyrhyncha</i>	0	0	0	0	1	1	0		2.3	23	Non-migrant	Itaipú dam
<i>Galeocharax humeralis</i>	1	1	0	0	0	0	0		4.01	30.5	Non-migrant	
<i>Galeocharax knerii</i>	1	1	1	1	1	1	1		3.96	22	Non-migrant	
<i>Geophagus brasiliensis</i>	0	0	1	1	1	1	1		2.57	28	Non-migrant	
<i>Geophagus proximus</i>	0	0	1	1	1	1	1		2.22	22.5	Non-migrant	fish-farming / aquarium trade
<i>Glandulocauda melanopleura</i>	0	0	1	1	1	1	1		2.94	5.5	Non-migrant	
<i>Glanidium cesarpintoi</i>	0	0	1	1	1	1	1		3.32	9.1	Non-migrant	
<i>Gymnocorymbus ternetzi</i>	1	1	0	0	1	0	0		3.12	7.5	Non-migrant	aquarium trade
<i>Gymnogeophagus australis</i>	1	1	1	1	1	1	1		3.34	15.5	Non-migrant	
<i>Gymnogeophagus balzanii</i>	1	1	0	0	0	0	0		3.33	12	Non-migrant	
<i>Gymnogeophagus che</i>	1	1	0	0	0	0	0		3.33	11.6	Non-migrant	
<i>Gymnogeophagus meridionalis</i>	1	1	0	0	0	0	0		3.28	8.8	Non-migrant	
<i>Gymnogeophagus setequedas</i>	1	1	1	1	1	1	1	Brazil	3.3	9.8	Non-migrant	
<i>Gymnorhamphichthys hypostomus</i>	1	1	0	0	1	0	1		3.15	21.5	Non-migrant	Itaipú dam
<i>Gymnotus carapo</i>	1	1	1	1	1	1	1		2.99	76	Non-migrant	
<i>Gymnotus inaequilabius</i>	1	1	0	0	1	0	0		3.25	30	Non-migrant	unknown
<i>Gymnotus pantanal</i>	1	1	0	1	1	1	1		3.27	25.1	Non-migrant	Itaipú dam
<i>Gymnotus pantherinus</i>	0	0	1	1	1	1	1		3.19	13.4	Non-migrant	
<i>Gymnotus paraguensis</i>	1	1	0	0	1	1	1		3.24	24	Non-migrant	Itaipú dam / fishing - fish bait
<i>Gymnotus sylvius</i>	0	0	1	1	1	1	1		3.14	8.4	Non-migrant	
<i>Harttia gracilis</i>	0	0	1	1	1	1	1		2.52	10.1	Non-migrant	
<i>Hasemania crenuchoides</i>	0	0	1	1	1	1	1		3	6.7	Non-migrant	
<i>Hasemania hansenii</i>	0	0	1	1	1	1	1		3	3.1	Non-migrant	
<i>Hemigrammus marginatus</i>	1	1	1	1	1	1	1		2.81	4.5	Non-migrant	
<i>Hemigrammus parana</i>	0	0	1	1	1	1	1		3.01	3.1	Non-migrant	
<i>Hemiodus orthonops</i>	1	1	0	0	1	1	0		2.66	25	Non-migrant	Itaipú dam / piracema channel
<i>Hemiodus semitaeniatus</i>	1	1	0	0	0	0	0		2.71	20	Non-migrant	
<i>Hemisorubim platyrhynchos</i>	1	1	1	1	1	1	1		4.5	52.5	Migratory	
<i>Heptapterus multiradiatus</i>	0	0	1	1	1	1	1		3.27	9.6	Non-migrant	
<i>Heptapterus mustelinus</i>	1	1	0	0	1	1	0		3.39	20.9	Non-migrant	Itaipú dam
<i>Hisonotus depressicauda</i>	0	0	1	1	1	1	1		2	5	Non-migrant	
<i>Hisonotus depressinotus</i>	0	0	1	1	1	1	1		2.36	3	Non-migrant	
<i>Hisonotus francirochai</i>	0	0	1	1	1	1	1		2	3.6	Non-migrant	
<i>Hisonotus insperatus</i>	0	0	1	1	1	1	1		2.35	3	Non-migrant	
<i>Hisonotus maculipinnis</i>	1	1	0	0	0	0	0		2.05	4	Non-migrant	
<i>Hisonotus nigricauda</i>	1	1	0	0	0	0	0		2	5	Non-migrant	
<i>Hisonotus paulinus</i>	0	0	1	1	1	1	1		2.05	4	Non-migrant	
<i>Hollandichthys multifasciatus</i>	0	0	1	1	1	1	1		3.03	9.6	Non-migrant	
<i>Homodiaetetus anisitsi</i>	1	1	0	0	0	0	0		3.14	4.2	Non-migrant	

<i>Hoplerythrinus unitaeniatus</i>	1	1	0	0	1	0	1		3.41	25	Non-migrant	Fishing / Itaipú dam
<i>Hoplias aff. malabaricus</i>	1	1	1	1	1	1	1		4.5	55.2	Non-migrant	
<i>Hoplias microcephalus</i>	0	0	1	1	1	1	1		3.97	35.6	Non-migrant	
<i>Hoplosternum littorale</i>	1	1	1	1	1	1	1		2.68	24	Non-migrant	
<i>Hyphessobrycon anisitsi</i>	1	1	1	1	1	1	1		2.98	6	Non-migrant	
<i>Hyphessobrycon arianae</i>	1	1	0	0	0	0	0		2.96	2.4	Non-migrant	
<i>Hyphessobrycon balbus</i>	0	0	1	1	1	1	1		2.88	6	Non-migrant	
<i>Hyphessobrycon bifasciatus</i>	0	0	1	1	1	1	1		2.91	4.7	Non-migrant	
<i>Hyphessobrycon coelestinus</i>	0	0	1	1	1	1	1		2.96	2.9	Non-migrant	
<i>Hyphessobrycon duragenys</i>	0	0	1	1	1	1	1	Brazil	2.87	6.9	Non-migrant	
<i>Hyphessobrycon elachys</i>	1	1	0	0	0	0	0		2.99	2	Non-migrant	
<i>Hyphessobrycon eques</i>	1	1	1	1	1	1	1		3.06	4	Non-migrant	aquarium trade
<i>Hyphessobrycon flammeus</i>	0	0	0	0	1	0	0		2.89	2.5	Non-migrant	aquarium trade
<i>Hyphessobrycon guarani</i>	1	1	0	0	0	0	0		2.93	3.1	Non-migrant	
<i>Hyphessobrycon igneus</i>	1	1	0	0	0	0	0	Argentina	2.92	3.4	Non-migrant	
<i>Hyphessobrycon meridionalis</i>	1	1	0	0	0	0	0	Argentina	2.98	4.6	Non-migrant	
<i>Hyphessobrycon reticulatus</i>	1	1	1	1	1	1	1		2.88	4.9	Non-migrant	
<i>Hyphessobrycon wajat</i>	1	1	0	0	0	0	0		2.93	3.1	Non-migrant	
<i>Hypophthalmus edentatus</i>	1	1	0	0	1	1	1	Argentina	2.91	57.5	Non-migrant	Itaipú dam
<i>Hypophthalmus oremaculatus</i>	1	1	0	0	0	0	0	Argentina	3.4	50	Non-migrant	
<i>Hypoptopoma inexpectatum</i>	1	1	0	0	0	0	0		2	7.1	Non-migrant	
<i>Hypostomus alatus</i>	1	1	0	0	0	0	0		2.03	27	Non-migrant	
<i>Hypostomus albopunctatus</i>	1	1	1	1	1	1	1		2.03	27	Non-migrant	
<i>Hypostomus ancistroides</i>	0	0	1	1	1	1	1		2	21	Non-migrant	
<i>Hypostomus auroguttatus</i>	1	1	0	0	0	0	0		2.07	28.6	Non-migrant	
<i>Hypostomus boulengeri</i>	1	1	0	0	0	0	0		2.06	24.5	Non-migrant	
<i>Hypostomus brevis</i>	0	0	1	1	1	1	1		2.48	7.4	Non-migrant	
<i>Hypostomus cochliodon</i>	1	1	0	0	1	0	1		2.08	23	Non-migrant	unknown / Itaipú dam
<i>Hypostomus commersoni</i>	1	1	0	0	1	0	1		2	60.5	Non-migrant	unknown / Itaipú dam
<i>Hypostomus denticulatus</i>	0	0	1	1	1	1	1		2.15	19.1	Non-migrant	
<i>Hypostomus dlouhyi</i>	1	1	0	0	1	0	0		2.06	24.5	Non-migrant	unknown
<i>Hypostomus fluviatilis</i>	0	0	1	1	1	1	1		2.2	16.5	Non-migrant	
<i>Hypostomus heraldoi</i>	0	0	1	1	1	1	1		2.07	23.6	Non-migrant	
<i>Hypostomus hermanni</i>	0	0	1	1	1	1	1		2.14	24	Non-migrant	
<i>Hypostomus iheringi</i>	0	0	1	1	1	1	1		2.32	11.6	Non-migrant	
<i>Hypostomus lexi</i>	0	0	1	1	1	1	1		2	46	Non-migrant	
<i>Hypostomus luteomaculatus</i>	1	1	0	0	0	0	0		2.01	28	Non-migrant	
<i>Hypostomus margaritifer</i>	0	0	1	1	1	1	1		2.02	33	Non-migrant	
<i>Hypostomus meleagris</i>	0	0	1	1	1	1	1		2	30	Non-migrant	



<i>Hypostomus microstomus</i>	1	1	0	1	1	1	1		2.07	24	Non-migrant	Itaipú dam
<i>Hypostomus multidentis</i>	0	0	1	1	1	1	1		2.13	19.8	Non-migrant	
<i>Hypostomus nigromaculatus</i>	0	0	1	1	1	1	1		2.36	10.2	Non-migrant	
<i>Hypostomus paulinus</i>	0	0	1	1	1	1	1		2.28	13.1	Non-migrant	
<i>Hypostomus piratatu</i>	1	1	0	0	0	0	0		2.02	27.5	Non-migrant	
<i>Hypostomus regani</i>	1	1	1	1	1	1	1		2	39.7	Non-migrant	
<i>Hypostomus scaphycephus</i>	0	0	1	1	1	1	1		2.74	3.5	Non-migrant	
<i>Hypostomus strigaticeps</i>	0	0	1	1	1	1	1		2.23	15	Non-migrant	
<i>Hypostomus ternetzi</i>	1	1	0	0	1	0	1		2.01	34.3	Non-migrant	unknown / Itaipú dam
<i>Hypostomus tietensis</i>	0	0	1	1	1	1	1		2.29	12.5	Non-migrant	
<i>Hypostomus topavae</i>	0	0	1	1	1	1	1		2	70	Non-migrant	
<i>Hypostomus variipictus</i>	0	0	1	1	1	1	1		2	37	Non-migrant	
<i>Hypostomus variostictus</i>	1	1	0	0	0	0	0		2.64	5.7	Non-migrant	
<i>Iheringichthys labrosus</i>	1	1	1	1	1	1	1		2.94	29.7	Non-migrant	
<i>Imparfinis borodini</i>	0	0	1	1	1	1	1		2.97	15.7	Non-migrant	
<i>Imparfinis mirini</i>	0	0	1	1	1	1	1		2.98	8.5	Non-migrant	
<i>Imparfinis mishky</i>	1	1	0	0	0	0	0		2.98	8.5	Non-migrant	
<i>Imparfinis schubarti</i>	0	0	1	1	1	1	1		2.98	9.3	Non-migrant	
<i>Isbrueckerichthys calvus</i>	0	0	1	1	1	1	1		2.36	9	Non-migrant	
<i>Isbrueckerichthys saxicola</i>	0	0	1	1	1	1	1		2.37	8.8	Non-migrant	
<i>Ituglanis eichorniarum</i>	1	1	0	0	0	0	0		3.17	5	Non-migrant	
<i>Jenynsia multidentata</i>	1	1	0	0	0	0	0		2.9	6.56	Non-migrant	
<i>Knodus moenkhausii</i>	1	1	0	0	1	1	0		2.62	4.5	Non-migrant	Itaipú dam
<i>Kolpotocheiroduon theloura</i>	0	0	1	1	1	1	1		2.66	3	Non-migrant	
<i>Laetacara dorsigera</i>	1	1	0	0	0	0	0		3.09	6	Non-migrant	
<i>Lepidosiren paradoxa</i>	1	1	0	0	0	0	0		3.11	125	Non-migrant	
<i>Leporellus vittatus</i>	1	1	1	1	1	1	1		2.25	30	Non-migrant	
<i>Leporinus acutidens</i>	1	1	0	0	0	0	0		2.05	33	Non-migrant	
<i>Leporinus aquapeiensis</i>	0	0	1	1	1	1	1		2.17	18.8	Non-migrant	
<i>Leporinus amblyrhynchus</i>	0	0	1	1	1	1	1		2.16	19.6	Non-migrant	
<i>Leporinus elongatus</i>	1	1	1	1	1	1	1		2	39.8	Migratory	
<i>Leporinus friderici</i>	1	1	1	1	1	1	1		3.26	40	Non-migrant	
<i>Leporinus lacustris</i>	1	1	1	1	1	1	1		3.72	20.3	Non-migrant	
<i>Leporinus macrocephalus</i>	1	1	0	0	1	0	0		2	60	Migratory	fish-farming
<i>Leporinus microphthalmus</i>	0	0	1	1	1	1	1		2.33	11.8	Non-migrant	
<i>Leporinus obtusidens</i>	1	1	1	1	1	1	1		2	76	Migratory	
<i>Leporinus octofasciatus</i>	1	1	1	1	1	1	1		2	23.5	Non-migrant	
<i>Leporinus paranensis</i>	0	0	1	1	1	1	1		2.23	16	Non-migrant	
<i>Leporinus striatus</i>	1	1	1	1	1	1	1	Argentina	2	25	Non-migrant	

<i>Leporinus tigrinus</i>	0	0	1	1	1	1	1		2.14	25	Non-migrant	
<i>Lepthoplosternum pectorale</i>	1	1	1	1	1	1	1		2.92	6	Non-migrant	
<i>Lophiobrycon weitzmani</i>	0	0	1	1	1	1	1		3.27	2.9	Non-migrant	
<i>Loricaria apeltogaster</i>	1	1	0	0	0	0	0		2.27	26	Non-migrant	
<i>Loricaria lentiginosa</i>	0	0	1	1	1	1	1		2.09	51.4	Non-migrant	
<i>Loricaria piracicabae</i>	0	0	1	1	1	1	1		2.38	17	Non-migrant	
<i>Loricaria simillima</i>	1	1	0	0	1	1	0		2.37	18	Non-migrant	Itaipú dam
<i>Loricariichthys anus</i>	1	1	0	0	0	0	0		2.59	46	Non-migrant	
<i>Loricariichthys labialis</i>	1	1	0	0	0	0	0		2.59	22	Non-migrant	
<i>Loricariichthys melanocheilus</i>	1	1	0	0	0	0	0		2.6	20.9	Non-migrant	
<i>Loricariichthys platymetopon</i>	1	1	0	0	1	1	1		2.45	30	Non-migrant	Itaipú dam
<i>Loricariichthys rostratus</i>	1	1	0	0	1	1	1		2.55	27.5	Non-migrant	Itaipú dam
<i>Luciopimelodus pati</i>	1	1	0	0	0	0	0		4.31	103	Non-migrant	
<i>Markiana nigripinnis</i>	1	1	0	0	0	0	0		3	10.4	Non-migrant	
<i>Megalancistrus parananus</i>	1	1	1	1	1	1	1		2	58.8	Non-migrant	
<i>Megalebias elongatus</i>	1	1	0	0	0	0	0		3.41	22	Non-migrant	
<i>Megalechis thoracata</i>	1	1	0	0	1	1	0		2.88	12.4	Non-migrant	Itaipú dam
<i>Megalonema argentina</i>	1	1	0	0	0	0	0		3.93	27.1	Non-migrant	
<i>Megalonema pauciradiatum</i>	1	1	0	0	0	0	0		3.28	3.8	Non-migrant	
<i>Megalonema platanum</i>	1	1	1	0	1	0	0		3.95	40	Non-migrant	unknown
<i>Mesonauta festivus</i>	1	1	0	0	0	0	0		2.51	8.2	Non-migrant	
<i>Metynnis maculatus</i>	1	1	0	0	1	1	0		2.9	18	Non-migrant	Itaipú dam / unknown
<i>Metynnis mola</i>	1	1	0	0	1	1	0		2.89	15	Non-migrant	Itaipú dam / unknown
<i>Microglanis garavelloii</i>	0	0	1	1	1	1	1		3.39	4.2	Non-migrant	
<i>Microglanis parahybae</i>	1	1	0	0	0	0	0		3.47	8	Non-migrant	
<i>Microlepidogaster perforatus</i>	0	0	1	1	1	1	1		2	5	Non-migrant	
<i>Microlepidogaster longiculla</i>	0	0	1	1	1	1	1		2	5	Non-migrant	
<i>Micropterus salmoides</i>	0	0	0	0	1	0	0		3.84	97	Non-migrant	fishing / fish-farming
<i>Mimagoniates microlepis</i>	0	0	1	1	1	1	1		3.2	6.1	Non-migrant	
<i>Moenkhausia dichroua</i>	1	1	0	0	0	0	0		3.45	10	Non-migrant	
<i>Moenkhausia forestii</i>	0	0	1	1	1	1	1		3	3.8	Non-migrant	
<i>Moenkhausia intermedia</i>	1	1	1	1	1	1	1	Argentina	2.65	8	Non-migrant	
<i>Moenkhausia sanctaefilomenae</i>	1	1	1	1	1	1	1		2.95	7	Non-migrant	
<i>Myleus levis</i>	1	1	0	0	0	0	0		2	20	Migratory	
<i>Myleus tiete</i>	1	1	1	1	1	1	1	Brazil	2.16	15.2	Migratory	
<i>Mylossoma duriventre</i>	1	1	1	1	1	1	1		2.84	25	Migratory	
<i>Neoplecostomus corumba</i>	0	0	1	1	1	1	1		2.41	7.8	Non-migrant	
<i>Neoplecostomus paranensis</i>	0	0	1	1	1	1	1		2.35	9.3	Non-migrant	
<i>Neoplecostomus selene</i>	0	0	1	1	1	1	1		2.31	10.2	Non-migrant	

<i>Neoplecostomus yapo</i>	0	0	1	1	1	1	1		2.28	11	Non-migrant	
<i>Odontesthes bonariensis</i>	1	1	0	0	1	1	0		2.57	50	Non-migrant	Itaipú dam
<i>Odontostilbe microcephala</i>	1	1	1	1	1	1	1		2.42	4.6	Non-migrant	
<i>Odontostilbe paraguayensis</i>	1	1	0	0	0	0	0		2.55	4	Non-migrant	
<i>Odontostilbe pequirá</i>	1	1	0	0	0	0	0		2.44	5.6	Non-migrant	
<i>Odontostilbe stenodon</i>	0	0	1	1	1	1	1		2.63	3.3	Non-migrant	
<i>Oligosarcus jenynsii</i>	1	1	0	0	0	0	0		3.97	31	Non-migrant	
<i>Oligosarcus menezesi</i>	1	1	0	0	0	0	0		3.75	13.8	Non-migrant	
<i>Oligosarcus oligolepis</i>	1	1	0	0	0	0	0		3.15	2.5	Non-migrant	
<i>Oligosarcus paranensis</i>	1	1	1	1	1	1	1		3.89	20.5	Non-migrant	
<i>Oligosarcus pintoí</i>	0	0	1	1	1	1	1		3.45	8.4	Non-migrant	
<i>Oligosarcus planaltinae</i>	0	0	1	1	1	1	1		3.64	9.9	Non-migrant	
<i>Oreochromis niloticus</i>	0	1	0	0	1	0	0		2	60	Non-migrant	fish-farming
<i>Otocinclus flexilis</i>	1	1	0	0	0	0	0		2	5.5	Non-migrant	
<i>Otocinclus mimulus</i>	1	1	0	0	0	0	0		2	4.3	Non-migrant	
<i>Otocinclus vestitus</i>	1	1	0	0	0	0	0		2.29	3.2	Non-migrant	
<i>Otocinclus vittatus</i>	1	1	0	0	0	0	0		2.47	3.3	Non-migrant	
<i>Otothyropsis marapoama</i>	0	0	1	1	1	1	1		2	3.8	Non-migrant	
<i>Oxydoras eigenmanni</i>	1	1	0	0	1	1	1		2.83	10	Non-migrant	Itaipú dam
<i>Oxydoras kneri</i>	1	1	0	0	0	0	0		3.17	70	Non-migrant	
<i>Pachyurus bonariensis</i>	1	1	0	0	0	0	0		3.51	22.6	Non-migrant	
<i>Pamphorichthys hollandi</i>	0	0	1	1	1	1	1		2.99	2.5	Non-migrant	
<i>Paraloricaria agastor</i>	1	1	0	0	0	0	0		2.5	10.8	Non-migrant	
<i>Paraloricaria vetula</i>	1	1	0	0	0	0	0		2.12	55.4	Non-migrant	
<i>Parapimelodus valenciennis</i>	1	1	0	0	0	0	0		3.7	17	Non-migrant	
<i>Parastegophilus maculatus</i>	1	1	0	0	0	0	0		4.2	6	Non-migrant	
<i>Parastegophilus paulensis</i>	0	0	1	1	1	1	1		3.18	5.4	Non-migrant	
<i>Paravandellia oxyptera</i>	1	1	1	1	1	1	1		3.08	2.8	Non-migrant	
<i>Pareorhina carrancas</i>	0	0	1	1	1	1	1		2.65	4.1	Non-migrant	
<i>Parodon moreirai</i>	0	0	1	1	1	1	1		2.32	11.8	Non-migrant	
<i>Parodon nasus</i>	1	1	1	1	1	1	1		2.3	12.7	Non-migrant	
<i>Pellona flavipinnis</i>	1	1	0	0	0	0	0		4.5	73	Non-migrant	
<i>Phalloceros caudimaculatus</i>	1	1	0	0	0	0	0		2.82	3.5	Non-migrant	
<i>Phalloceros harpagos</i>	1	1	1	1	1	1	1		2.5	3.4	Non-migrant	
<i>Phalloceros reisi</i>	0	0	1	1	1	1	1		2.95	2.7	Non-migrant	
<i>Phallotorynus dispilos</i>	1	1	0	0	0	0	0		2.98	1.8	Non-migrant	
<i>Phallotorynus fasciolatus</i>	0	0	1	1	1	1	1	Brazil	2.98	2.5	Non-migrant	
<i>Phallotorynus jucundus</i>	0	0	1	1	1	1	1	Brazil	2.98	2.5	Non-migrant	
<i>Phallotorynus pankalos</i>	0	0	1	1	1	1	1		2.98	2.8	Non-migrant	

<i>Phallotorynus victoriae</i>	1	1	1	1	1	1	1		2.98	2.3	Non-migrant	
<i>Phenacorhamdia tenebrosa</i>	0	0	1	1	1	1	1		3.22	6.7	Non-migrant	
<i>Phenacorhamdia unifasciata</i>	0	0	1	1	1	1	1		3.2	6.2	Non-migrant	
<i>Piabina anhembi</i>	0	0	1	1	1	1	1		3	6.5	Non-migrant	
<i>Piabina argentea</i>	1	1	1	1	1	1	1		3	6.8	Non-migrant	
<i>Piaractus mesopotamicus</i>	1	1	1	1	1	1	1		2	40.5	Migratory	
<i>Pimelodella avanhandavae</i>	0	0	1	1	1	1	1		3.46	9.6	Non-migrant	
<i>Pimelodella boschmai</i>	0	0	1	1	1	1	1		3.53	10	Non-migrant	
<i>Pimelodella gracilis</i>	1	1	1	1	1	1	1		3.24	18	Non-migrant	
<i>Pimelodella howesi</i>	1	1	0	0	0	0	0		3.46	7.9	Non-migrant	
<i>Pimelodella meeki</i>	0	0	1	1	1	1	1		3.48	10.2	Non-migrant	
<i>Pimelodella rudolphi</i>	0	0	1	1	1	1	1		3.55	10.5	Non-migrant	
<i>Pimelodella taenioptera</i>	1	1	0	0	1	1	0		3.56	12.1	Non-migrant	Itaipú dam / piracema channel
<i>Pimelodus absconditus</i>	1	1	0	0	0	0	0		3.48	28.7	Non-migrant	
<i>Pimelodus albicans</i>	1	1	0	0	0	0	0		3.36	57	Non-migrant	
<i>Pimelodus argenteus</i>	1	1	0	0	0	0	0		3.27	25	Non-migrant	
<i>Pimelodus brevis</i>	1	1	0	0	0	0	0		3.31	28.5	Non-migrant	
<i>Pimelodus fur</i>	0	0	0	0	1	0	0		3.28	17	Non-migrant	unknown
<i>Pimelodus heraldoi</i>	0	0	1	1	1	1	1		3.26	18	Non-migrant	
<i>Pimelodus maculatus</i>	1	1	1	1	1	1	1		2.87	51	Migratory	
<i>Pimelodus mysteriosus</i>	1	1	0	0	0	0	0		3.24	14.3	Non-migrant	
<i>Pimelodus ornatus</i>	1	1	0	0	1	1	1		3.34	38.5	Migratory	Itaipú dam
<i>Pimelodus paranaensis</i>	0	0	1	1	1	1	1		3.28	23.1	Non-migrant	
<i>Pimelodus platicirris</i>	0	0	1	1	1	1	1		3.28	16	Non-migrant	
<i>Pinirampus pirinampu</i>	1	1	1	1	1	1	1		4.5	120	Migratory	
<i>Plagioscion squamosissimus</i>	0	1	0	0	1	0	0		4.35	80	Non-migrant	fish-farming / fish stocking
<i>Plagioscion ternetzi</i>	1	1	0	0	0	0	0		3.92	39	Non-migrant	
<i>Planaltina britskii</i>	0	0	1	1	1	1	1		3.23	4.5	Non-migrant	
<i>Planaltina glandipedis</i>	0	0	1	1	1	1	1		3.23	4.5	Non-migrant	
<i>Planaltina myersi</i>	0	0	1	1	1	1	1		3.23	4.6	Non-migrant	
<i>Platydoras armatulus</i>	1	1	0	0	1	1	1		2.76	20	Non-migrant	Itaipú dam
<i>Platydoras costatus</i>	1	1	0	0	0	0	0	Argentina	3.04	24	Non-migrant	
<i>Poecilia reticulata</i>	0	0	0	0	1	0	0		3.2	6	Non-migrant	mosquito control
<i>Poecilia vivipara</i>	1	1	1	1	1	0	0		3.2	4	Non-migrant	mosquito control
<i>Poptella paraguayensis</i>	1	1	0	0	0	0	0		3.22	7	Non-migrant	
<i>Potamorhina squamoralevis</i>	1	1	0	0	0	0	0		2.02	23.4	Non-migrant	
<i>Potamorrhaphis eigenmanni</i>	1	1	0	0	0	0	0	Argentina	3.9	22.8	Non-migrant	
<i>Potamotrygon brachyura</i>	1	1	0	0	0	0	0		3.2	95	Non-migrant	
<i>Potamotrygon castexi</i>	1	1	0	0	0	0	0		3.2	60	Non-migrant	

<i>Potamotrygon falkneri</i>	1	1	0	0	1	1	1		3.2	47	Non-migrant	Itaipú dam
<i>Potamotrygon hystrix</i>	1	1	0	0	0	0	0		3.2	40	Non-migrant	
<i>Potamotrygon motoro</i>	1	1	0	0	1	1	1		3.2	50	Non-migrant	Itaipú dam
<i>Potamotrygon schuhmacheri</i>	1	1	0	0	0	0	0		3.2	25	Non-migrant	
<i>Prionobrama paraguayensis</i>	1	1	0	0	0	0	0		3	5	Non-migrant	
<i>Prochilodus lineatus</i>	1	1	1	1	1	1	1		2.18	80	Migratory	
<i>Prochilodus vimboides</i>	0	0	1	1	1	1	1		2.04	33	Non-migrant	
<i>Proloricaria prolixa</i>	0	0	1	1	1	1	1		3	35	Non-migrant	
<i>Psectrogaster curviventris</i>	1	1	0	0	0	0	0		2	17.1	Non-migrant	
<i>Psellogrammus kennedyi</i>	1	1	0	0	1	0	0		3	5.9	Non-migrant	unknown
<i>Pseudobunocephalus iheringii</i>	1	1	0	0	0	0	0		3.1	5.9	Non-migrant	
<i>Pseudobunocephalus rugosus</i>	1	1	0	0	0	0	0		3.05	3	Non-migrant	
<i>Pseudocorynopoma doriae</i>	1	1	0	0	0	0	0		3.3	6.2	Non-migrant	
<i>Pseudocorynopoma heterandria</i>	0	0	1	1	1	1	1		3.28	5.6	Non-migrant	
<i>Pseudohemiodon laticeps</i>	1	1	0	0	0	0	0		2.23	29.8	Non-migrant	
<i>Pseudopimelodus aff. pulcher</i>	0	0	1	1	1	1	1		3.39	8.7	Non-migrant	
<i>Pseudopimelodus mangurus</i>	1	1	1	1	1	1	1		3.93	69	Non-migrant	
<i>Pseudoplatystoma corruscans</i>	1	1	1	1	1	1	1		4.5	166	Migratory	
<i>Pseudoplatystoma fasciatum</i>	1	1	1	1	1	1	1		4.38	104	Migratory	
<i>Pseudotocinclus tietensis</i>	0	0	1	1	1	1	1		2	6	Non-migrant	
<i>Pseudotylorus angusticeps</i>	1	1	0	0	0	0	0	Argentina	3.99	29.8	Non-migrant	
<i>Pterodoras granulosus</i>	1	1	0	0	1	1	1		2.55	70	Migratory	Itaipú dam
<i>Pterygoplichthys anisitsi</i>	1	1	1	1	1	1	1		2.06	42	Non-migrant	Itaipú dam
<i>Pygocentrus nattereri</i>	1	1	1	1	1	1	1		3.72	50	Non-migrant	
<i>Pyrrhulina australis</i>	1	1	1	1	1	1	1		3.23	5	Non-migrant	
<i>Ramnogaster melanostoma</i>	1	1	0	0	0	0	0		3.2	10	Non-migrant	
<i>Rhamdella cainguae</i>	1	1	0	0	0	0	0		3.35	15.8	Non-migrant	
<i>Rhamdella longipinnis</i>	0	0	1	1	1	1	1		3.26	8.8	Non-migrant	
<i>Rhamdia quelen</i>	1	1	1	1	1	1	1		3.16	47.4	Non-migrant	
<i>Rhamdiopsis microcephala</i>	0	0	1	1	1	1	1	Brazil	3.24	7.8	Non-migrant	
<i>Rhamphichthys hahni</i>	1	1	0	0	1	1	1		3.16	26.7	Non-migrant	Itaipú dam
<i>Rhaphiodon vulpinus</i>	1	1	1	1	1	1	1		4.5	80	Migratory	
<i>Rhinelepis aspera</i>	0	0	1	1	1	1	1		2.08	33	Migratory	
<i>Rhinelepis strigosa</i>	1	1	0	0	0	0	0		2	40	Non-migrant	
<i>Rhinodoras dorbignyi</i>	1	1	1	1	1	1	1		2.69	50	Non-migrant	
<i>Ricola macrops</i>	1	1	0	0	0	0	0		2.32	21	Non-migrant	
<i>Rineloricaria latirostris</i>	0	0	1	1	1	1	1		2.23	36	Non-migrant	
<i>Rineloricaria microlepidogaster</i>	1	1	0	0	0	0	0		2.35	19.3	Non-migrant	
<i>Rineloricaria misionera</i>	1	1	0	0	0	0	0		2.53	9.74	Non-migrant	

<i>Rineloricaria pentamaculata</i>	0	0	1	1	1	1	1		2.44	10	Non-migrant	
<i>Rivulus apiamici</i>	0	0	1	1	1	1	1		3.12	3	Non-migrant	
<i>Rivulus egens</i>	0	0	1	1	1	1	1		3.21	3.3	Non-migrant	
<i>Rivulus fauicreticulatus</i>	0	0	1	1	1	1	1		3.12	3	Non-migrant	
<i>Rivulus formosensis</i>	0	0	1	1	1	1	1		3.15	3.3	Non-migrant	
<i>Rivulus giarettai</i>	0	0	1	1	1	1	1		3.17	3.2	Non-migrant	
<i>Rivulus illuminatus</i>	0	0	1	1	1	1	1		3.14	2.9	Non-migrant	
<i>Rivulus pictus</i>	0	0	1	1	1	1	1		3.19	5	Non-migrant	
<i>Rivulus pinima</i>	0	0	1	1	1	1	1		3.12	3	Non-migrant	
<i>Rivulus punctatus</i>	1	1	0	0	0	0	0		3.11	3.5	Non-migrant	
<i>Rivulus rossoi</i>	0	0	1	1	1	1	1		3.21	3.5	Non-migrant	
<i>Rivulus rutilicaudus</i>	0	0	1	1	1	1	1		3.21	3.5	Non-migrant	
<i>Rivulus scalaris</i>	0	0	1	1	1	1	1		3.21	3.5	Non-migrant	
<i>Rivulus vittatus</i>	0	0	1	1	1	1	1		3.21	3.5	Non-migrant	
<i>Roeboides descavadensis</i>	1	1	0	0	1	1	1		3.73	8.9	Non-migrant	Itaipú dam
<i>Roeboides microlepis</i>	0	0	1	1	1	1	1		4.03	20	Non-migrant	
<i>Roeboides prognathus</i>	1	1	0	0	0	0	0		4.11	14	Non-migrant	
<i>Salminus brasiliensis</i>	1	1	1	1	1	1	1		3.79	100	Migratory	
<i>Salminus hilarii</i>	0	1	1	1	1	1	1		3	50	Migratory	
<i>Satanoperca pappaterra</i>	0	0	0	0	1	0	0		2.77	19.2	Non-migrant	fish-farming
<i>Schizodon altoparanae</i>	0	0	1	1	1	1	1		2.49	23	Non-migrant	
<i>Schizodon borellii</i>	1	1	1	1	1	1	1		2.45	30	Non-migrant	
<i>Schizodon intermedius</i>	0	0	1	1	1	1	1		2.45	28.7	Non-migrant	
<i>Schizodon isognathus</i>	1	1	0	0	0	0	0		2.48	35	Non-migrant	
<i>Schizodon nasutus</i>	1	1	1	1	1	1	1	Argentina	2.83	40.2	Non-migrant	
<i>Schizodon platae</i>	1	1	0	0	0	0	0		2.45	30	Non-migrant	
<i>Scleromystax macropterus</i>	0	0	1	1	1	1	1		2.94	8.7	Non-migrant	
<i>Serrapinnus calliurus</i>	1	1	0	0	0	0	0		2.62	4.4	Non-migrant	
<i>Serrapinnus heterodon</i>	0	0	1	1	1	1	1		2.49	4.1	Non-migrant	
<i>Serrapinnus notomelas</i>	0	0	1	1	1	1	1		2.21	3.6	Non-migrant	
<i>Serrasalmus maculatus</i>	1	1	1	1	1	1	1		4.07	26	Non-migrant	
<i>Serrasalmus marginatus</i>	1	1	0	1	1	1	1		3.55	27	Non-migrant	Itaipú dam
<i>Simpsonichthys boitonei</i>	0	0	1	1	1	1	1	Brazil	3.17	5.5	Non-migrant	
<i>Simpsonichthys nigromaculatus</i>	0	0	1	1	1	1	1		3.08	2.6	Non-migrant	
<i>Simpsonichthys parallelus</i>	0	0	1	1	1	1	1	Brazil	3.05	2.3	Non-migrant	
<i>Simpsonichthys santanae</i>	0	0	1	1	1	1	1	Brazil	3.07	3	Non-migrant	
<i>Sorubim lima</i>	1	1	0	0	1	0	1		4.09	54.2	Non-migrant	unknown / Itaipú dam
<i>Spatuloricaria evansii</i>	1	1	0	0	0	0	0		2.34	20	Non-migrant	
<i>Spintherobolus papilliferus</i>	0	0	1	1	1	1	1	Brazil	2.27	6.1	Non-migrant	

<i>Steindachneridion punctatum</i>	0	0	1	1	1	1	1		4.25	69.7	Migratory	
<i>Steindachneridion scriptum</i>	0	0	1	1	1	1	1	Brazil	4.27	90	Migratory	
<i>Steindachnerina biornata</i>	1	1	0	0	0	0	0		2	18.8	Non-migrant	
<i>Steindachnerina brevipinna</i>	1	1	0	0	1	1	1		2	20.5	Non-migrant	Itaipú dam
<i>Steindachnerina conspersa</i>	1	1	0	0	0	0	0		2	12.8	Non-migrant	
<i>Steindachnerina corumbae</i>	0	0	1	1	1	1	1		2	11.7	Non-migrant	
<i>Steindachnerina insculpta</i>	0	0	1	1	1	1	1		2.07	10.6	Non-migrant	
<i>Sternarchella curvioperculata</i>	0	0	1	1	1	1	1		3.29	25.3	Non-migrant	
<i>Sternarchorhynchus britskii</i>	0	0	1	1	1	1	1	Brazil	3.3	26.1	Non-migrant	
<i>Sternopygus macrurus</i>	0	0	1	1	1	1	1		3.22	141	Non-migrant	
<i>Sturisoma barbatum</i>	1	1	0	0	0	0	0		2.25	28	Non-migrant	
<i>Synbranchus marmoratus</i>	1	1	1	1	1	1	1		2.76	150	Non-migrant	
<i>Tatia neivai</i>	0	0	1	1	1	1	1		3.28	8.2	Non-migrant	
<i>Taunaya bifasciata</i>	0	0	1	1	1	1	1		3.33	14	Non-migrant	
<i>Tembeassu marauna</i>	0	0	1	1	1	1	1		3.26	19.6	Non-migrant	
<i>Tetragonopterus argenteus</i>	1	1	0	0	0	0	0		3.03	11.2	Non-migrant	
<i>Thoracocharax stellatus</i>	1	1	0	0	0	0	0		3.46	6.7	Non-migrant	
<i>Tilapia rendalli</i>	0	1	0	0	1	0	0		2.18	45	Non-migrant	fish-farming
<i>Trachelyopterus coriaceus</i>	0	0	1	1	1	1	1		3.43	18	Non-migrant	
<i>Trachelyopterus galeatus</i>	1	1	0	1	1	1	1		3.14	22	Non-migrant	Itaipú dam
<i>Trachelyopterus striatulus</i>	1	1	0	0	0	0	0		3.46	20	Non-migrant	
<i>Trachydoras paraguayensis</i>	1	1	0	0	1	1	1	Argentina	2.66	10.4	Non-migrant	Itaipú dam
<i>Trichomycterus brasiliensis</i>	0	0	0	0	1	0	0		3.2	13.5	Non-migrant	unknown
<i>Trichomycterus candidus</i>	0	0	1	1	1	1	1		3.2	7.5	Non-migrant	
<i>Trichomycterus diabolus</i>	0	0	1	1	1	1	1		3.2	6.1	Non-migrant	
<i>Trichomycterus johnsoni</i>	1	1	0	0	0	0	0	Argentina	3.2	1.6	Non-migrant	
<i>Trichomycterus maracaya</i>	0	0	1	1	1	1	1		3.27	5.1	Non-migrant	
<i>Trichomycterus paolence</i>	0	0	1	1	1	1	1		3.2	6.8	Non-migrant	
<i>Trichomycterus pauciradiatus</i>	0	0	1	1	1	1	1		3.14	5.2	Non-migrant	
<i>Triportheus nematurus</i>	1	1	0	0	1	1	0		2.8	18.3	Non-migrant	Itaipú dam
<i>Triportheus pantanensis</i>	1	1	0	0	0	0	0		2.8	15.8	Non-migrant	
<i>Xiphophorus helleri</i>	0	0	0	0	1	0	0		3.19	14	Non-migrant	aquarium trade
<i>Xiphophorus maculatus</i>	0	0	0	0	1	0	0		3.2	6	Non-migrant	aquarium trade
<i>Xyliphius barbatus</i>	1	1	0	0	0	0	0		3.14	9.2	Non-migrant	
<i>Xyliphius lombarderoi</i>	1	1	0	0	0	0	0		3.15	9.9	Non-migrant	
<i>Zungaro jahu</i>	1	1	1	1	1	1	1		4.48	140	Migratory	

292	299	258	259	332	297	288
LBTI	LATI	UBIJ	UBIL	UATI	UAIL	UAIJ

ctions - **LBTI**; Lower Paraná after introductions - **LATI**; Upper  
is - **UATI**; Upper Paraná after Itaipú dam (*sensu* Langeani et al.,  
ance migrants and non-migrants. The taxonomic classification

Family	Order	Class
Anostomidae	Characiformes	Actinopterygii
Acestrorhynchidae	Characiformes	Actinopterygii
Acestrorhynchidae	Characiformes	Actinopterygii
Cichlidae	Perciformes	Actinopterygii
Auchenipteridae	Siluriformes	Actinopterygii
Auchenipteridae	Siluriformes	Actinopterygii
Auchenipteridae	Siluriformes	Actinopterygii
Aspredinidae	Siluriformes	Actinopterygii
Doradidae	Siluriformes	Actinopterygii
Loricariidae	Siluriformes	Actinopterygii
Loricariidae	Siluriformes	Actinopterygii
Loricariidae	Siluriformes	Actinopterygii
Parodontidae	Characiformes	Actinopterygii
Parodontidae	Characiformes	Actinopterygii
Parodontidae	Characiformes	Actinopterygii
Parodontidae	Characiformes	Actinopterygii
Characidae	Characiformes	Actinopterygii
Characidae	Characiformes	Actinopterygii
Characidae	Characiformes	Actinopterygii
Cichlidae	Perciformes	Actinopterygii
Cichlidae	Perciformes	Actinopterygii
Cichlidae	Perciformes	Actinopterygii
Cichlidae	Perciformes	Actinopterygii
Aptereronotidae	Gymnotiformes	Actinopterygii
Aptereronotidae	Gymnotiformes	Actinopterygii
Aptereronotidae	Gymnotiformes	Actinopterygii
Aptereronotidae	Gymnotiformes	Actinopterygii





Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Aspredinidae	Siluriformes	Actiopterygii
Aspredinidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Achiridae	Pleuronectiformes	Actiopterygii
Cetopsidae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Crenuchidae	Characiformes	Actiopterygii
Crenuchidae	Characiformes	Actiopterygii
Crenuchidae	Characiformes	Actiopterygii
Crenuchidae	Characiformes	Actiopterygii
Crenuchidae	Characiformes	Actiopterygii
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Crenuchidae	Characiformes	Actiopterygii
Crenuchidae	Characiformes	Actiopterygii
Crenuchidae	Characiformes	Actiopterygii
Crenuchidae	Characiformes	Actiopterygii
Crenuchidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Clariidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Poeciliidae	Cyprinodontiformes	Actiopterygii
Poeciliidae	Cyprinodontiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii

Loricariidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
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Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Cyprinidae	Cypriniformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Doradidae	Siluriformes	Actiopterygii
Sternopygidae	Gymnotiformes	Actiopterygii
Sternopygidae	Gymnotiformes	Actiopterygii
Erythrinidae	Characiformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii

Loricariidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Auchenipteridae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Rhamphichthyidae	Gymnotiformes	Actiopterygii
Gymnotidae	Gymnotiformes	Actiopterygii
Gymnotidae	Gymnotiformes	Actiopterygii
Gymnotidae	Gymnotiformes	Actiopterygii
Gymnotidae	Gymnotiformes	Actiopterygii
Gymnotidae	Gymnotiformes	Actiopterygii
Gymnotidae	Gymnotiformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Hemiodontidae	Characiformes	Actiopterygii
Hemiodontidae	Characiformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Trichomycteridae	Siluriformes	Actiopterygii

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[illegible]

Anostomidae	Characiformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
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Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Pseudopimelodidae	Siluriformes	Actiopterygii
Pseudopimelodidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Centrarchidae	Perciformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii

[illegible]



Poeciliidae	Cyprinodontiformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Sciaenidae	Perciformes	Actiopterygii
Sciaenidae	Perciformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Doradidae	Siluriformes	Actiopterygii
Doradidae	Siluriformes	Actiopterygii
Poeciliidae	Cyprinodontiformes	Actiopterygii
Poeciliidae	Cyprinodontiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Belonidae	Beloniformes	Actiopterygii
Potamotrygonidae	Myliobatiformes	Elasmobranchii
Potamotrygonidae	Myliobatiformes	Elasmobranchii

Potamotrygonidae	Myliobatiformes	Elasmobranchii
Potamotrygonidae	Myliobatiformes	Elasmobranchii
Potamotrygonidae	Myliobatiformes	Elasmobranchii
Potamotrygonidae	Myliobatiformes	Elasmobranchii
Characidae	Characiformes	Actiopterygii
Prochilodontidae	Characiformes	Actiopterygii
Prochilodontidae	Characiformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Aspredinidae	Siluriformes	Actiopterygii
Aspredinidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Belonidae	Beloniformes	Actiopterygii
Doradidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Lebiasinidae	Characiformes	Actiopterygii
Clupeidae	Clupeiformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Heptapteridae	Siluriformes	Actiopterygii
Rhamphichthyidae	Gymnotiformes	Actiopterygii
Cynodontidae	Characiformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Doradidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii

Loricariidae	Siluriformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Anostomidae	Characiformes	Actiopterygii
Anostomidae	Characiformes	Actiopterygii
Anostomidae	Characiformes	Actiopterygii
Anostomidae	Characiformes	Actiopterygii
Anostomidae	Characiformes	Actiopterygii
Anostomidae	Characiformes	Actiopterygii
Callichthyidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Rivulidae	Cyprinodontiformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii

Pimelodidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Curimatidae	Characiformes	Actiopterygii
Apteronotidae	Gymnotiformes	Actiopterygii
Apteronotidae	Gymnotiformes	Actiopterygii
Sternopygidae	Gymnotiformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Synbranchidae	Synbranchiformes	Actiopterygii
Auchenipteridae	Siluriformes	Actiopterygii
Loricariidae	Siluriformes	Actiopterygii
Apteronotidae	Gymnotiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Gasteropelecidae	Characiformes	Actiopterygii
Cichlidae	Perciformes	Actiopterygii
Auchenipteridae	Siluriformes	Actiopterygii
Auchenipteridae	Siluriformes	Actiopterygii
Auchenipteridae	Siluriformes	Actiopterygii
Doradidae	Siluriformes	Actiopterygii
Trichomycteridae	Siluriformes	Actiopterygii
Trichomycteridae	Siluriformes	Actiopterygii
Trichomycteridae	Siluriformes	Actiopterygii
Trichomycteridae	Siluriformes	Actiopterygii
Trichomycteridae	Siluriformes	Actiopterygii
Trichomycteridae	Siluriformes	Actiopterygii
Trichomycteridae	Siluriformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Characidae	Characiformes	Actiopterygii
Poeciliidae	Cyprinodontiformes	Actiopterygii
Poeciliidae	Cyprinodontiformes	Actiopterygii
Aspredinidae	Siluriformes	Actiopterygii
Aspredinidae	Siluriformes	Actiopterygii
Pimelodidae	Siluriformes	Actiopterygii

Appendix 2 Chapter 2

Whittaker’s beta diversity index ( $\beta$ ) comparing all subsets of species distribution before and after introductions of non-native fishes. Lower Paraná before total introductions - **LBTI**; Lower Paraná after introductions - **LATI**; Upper Paraná before introductions (sensu Júlio Jr. et al., 2009) - **UBIJ**; Upper Paraná before introductions (sensu Langeani et al., 2007) - **UBIL**; Upper Paraná after total introductions - **UATI**; Upper Paraná after Itaipú dam (sensu Langeani et al., 2007) - **UAIL**; Upper Paraná after Itaipú dam (sensu Júlio Jr. et al., 2009) - **UAIJ**.

Subsets		$\beta$	
Lower Parana	Upper Parana	Before introduction	After introduction
LATI	UAIJ	0.7891	0.6965
LBTI	UAIJ	0.7666	0.6538
LATI	UAIL	0.7858	0.6706
LBTI	UAIL	0.7666	0.5744
LBTI	UATI	0.7698	0.5744
LBTI	UATI	0.7858	0.5744
LBTI	UATI	0.7891	0.5744
LBTI	UATI	0.7666	0.5594
LATI	UATI	0.7698	0.5594
LATI	UATI	0.7891	0.6965

### Appendix Chapter 3

List of fish species presence-absence data in the aquatic ecoregions of Lower and Upper Paraná River. The taxonomic classification and trophic level of species follows. FishBase (Froese & Pauly, 2012). Size - maximum body length (cm). Reproductive guild Tactic follows Agostinho et al. (2004)- **LM** - long migrant; **SME** - short migrant with external fecundation; **SMEP** - short migrants with external fecundation and parental care; **SMI** - short migrant with internal fecundation. Green fields represent natives in common to upper Paraná, Red fields represent invaders that had success and Blue fiels represents failed invaders.

Fauna of upper Paraná Ecoregion

Species	Trophic_level	Size	Reproduction	Family	Order
Ageneiosus militaris	3.76	30	SMI	Auchenipteridae	Siluriformes
Ancistrus cirrhosus	2	8.9	SMEP	Loricariidae	Siluriformes
Apareiodon affinis	2.21	14.3	SME	Parodontidae	Characiformes
Aphyocharax anisitsi	3.22	5.5	SME	Characidae	Characiformes
Aphyocharax dentatus	3.02	7.2	SME	Characidae	Characiformes
Astyanax eigenmanniorum	2.86	4.9	SME	Characidae	Characiformes
Astyanax fasciatus	2.75	16.8	SME	Characidae	Characiformes
Auchenipterus osteomystax	3.6	27	SMI	Auchenipteridae	Siluriformes
Australoheros facetus	3.33	19.3	SMEP	Cichlidae	Perciformes
Brycon orbignyanus	2.51	79	LM	Characidae	Characiformes
Bryconamericus iheringii	2	11	SME	Characidae	Characiformes
Bryconamericus stramineus	2.73	11.4	SME	Characidae	Characiformes
Callichthys callichthys	2.95	17	SME	Callichthyidae	Siluriformes
Cetopsis gobioides	3.64	10.9	SME	Cetopsidae	Siluriformes
Characidium zebra	3.2	6.5	SME	Crenuchidae	Characiformes
Corydoras aeneus	2.96	7.5	SME	Callichthyidae	Siluriformes
Corydoras paleatus	2.94	5.9	SME	Callichthyidae	Siluriformes
Crenicichla niederleini	3.23	23.5	SMEP	Cichlidae	Perciformes
Cyphocharax modestus	2	16.2	SME	Curimatidae	Characiformes
Eigenmannia trilineata	3.05	25	SME	Sternopygidae	Gymnotiformes
Eigenmannia virescens	3	35.8	SME	Sternopygidae	Gymnotiformes
Galeocharax knerii	3.96	22	SME	Characidae	Characiformes
Gymnogeophagus australis	3.34	15.5	SMEP	Cichlidae	Perciformes
Gymnogeophagus setequedas	3.3	9.8	SMEP	Cichlidae	Perciformes
Gymnotus carapo	2.99	76	SMEP	Gymnotidae	Gymnotiformes
Hemigrammus marginatus	2.81	4.5	SME	Characidae	Characiformes
Hemisorubim platyrhynchos	4.5	52.5	LM	Pimelodidae	Siluriformes
Hoplias aff. malabaricus	4.5	55.2	SMEP	Erythrinidae	Characiformes
Hoplosternum littorale	2.68	24	SME	Callichthyidae	Siluriformes
Hyphessobrycon anisitsi	2.98	6	SME	Characidae	Characiformes
Hyphessobrycon eques	3.06	4	SME	Characidae	Characiformes
Hyphessobrycon reticulatus	2.88	4.9	SME	Characidae	Characiformes
Hypostomus albopunctatus	2.03	27	SMEP	Loricariidae	Siluriformes
Hypostomus regani	2	39.7	SMEP	Loricariidae	Siluriformes
Iheringichthys labrosus	2.94	29.7	SME	Pimelodidae	Siluriformes

Leporellus vittatus	2.25	30	SME	Anostomidae	Characiformes
Leporinus elongatus	2	39.8	LM	Anostomidae	Characiformes
Leporinus friderici	3.26	40	SME	Anostomidae	Characiformes
Leporinus lacustris	3.72	20.3	SME	Anostomidae	Characiformes
Leporinus obtusidens	2	76	LM	Anostomidae	Characiformes
Leporinus octofasciatus	2	23.5	SME	Anostomidae	Characiformes
Leporinus striatus	2	25	SME	Anostomidae	Characiformes
Lepthoplosternum pectorale	2.92	6	SME	Callichthyidae	Siluriformes
Megalancistrus parananus	2	58.8	SMEP	Loricariidae	Siluriformes
Megalonema platanum	3.95	40	SME	Pimelodidae	Siluriformes
Moenkhausia intermedia	2.65	8	SME	Characidae	Characiformes
Moenkhausia sanctaefilomenae	2.95	7	SME	Characidae	Characiformes
Myleus tiete	2.16	15.2	LM	Characidae	Characiformes
Mylossoma duriventre	2.84	25	LM	Characidae	Characiformes
Odontostilbe microcephala	2.42	4.6	SME	Characidae	Characiformes
Oligosarcus paranensis	3.89	20.5	SME	Characidae	Characiformes
Paravandellia oxyptera	3.08	2.8	SME	Trichomycteridae	Siluriformes
Parodon nasus	2.3	12.7	SME	Parodontidae	Characiformes
Phalloceros harpagos	2.5	3.4	SMI	Poeciliidae	Cyprinodontiformes
Phallotorynus victoriae	2.98	2.3	SMI	Poeciliidae	Cyprinodontiformes
Piabina argentea	3	6.8	SME	Characidae	Characiformes
Piaractus mesopotamicus	2	40.5	LM	Characidae	Characiformes
Pimelodella gracilis	3.24	18	SME	Heptapteridae	Siluriformes
Pimelodus maculatus	2.87	51	SME	Pimelodidae	Siluriformes
Pinirampus pirinampu	4.5	120	LM	Pimelodidae	Siluriformes
Poecilia vivipara	3.2	4	SMI	Poeciliidae	Cyprinodontiformes
Prochilodus lineatus	2.18	80	LM	Prochilodontidae	Characiformes
Pseudopimelodus mangurus	3.93	69	SMEP	Pimelodidae	Siluriformes
Pseudoplatystoma corruscans	4.5	166	LM	Pimelodidae	Siluriformes
Pseudoplatystoma fasciatum	4.38	104	LM	Pimelodidae	Siluriformes
Pterygoplichthys anisitsi	2.06	42	SMEP	Loricariidae	Siluriformes
Pygocentrus nattereri	3.72	50	SMEP	Characidae	Characiformes
Pyrrhulina australis	3.23	5	SME	Lebiasinidae	Characiformes
Rhamdia quelen	3.16	47.4	SME	Heptapteridae	Siluriformes
Rhaphiodon vulpinus	4.5	80	LM	Cynodontidae	Characiformes
Rhinodoras dorbignyi	2.69	50	SME	Doradidae	Siluriformes
Salminus brasiliensis	3.79	100	LM	Characidae	Characiformes
Schizodon borellii	2.45	30	SME	Anostomidae	Characiformes
Schizodon nasutus	2.83	40.2	SME	Anostomidae	Characiformes
Serrasalmus maculatus	4.07	26	SMEP	Characidae	Characiformes
Synbranchus marmoratus	2.76	150	SME	Synbranchidae	Synbranchiformes
Zungaro jahu	4.48	140	LM	Pimelodidae	Siluriformes
Acestrorhynchus lacustris	4.2	27	SME	Acestrorhynchidae	Characiformes
Apareiodon ibitiensis	2.3	11.3	SME	Parodontidae	Characiformes
Apareiodon piracicabae	2.28	12	SME	Parodontidae	Characiformes
Apareiodon vladii	2.3	11.3	SME	Parodontidae	Characiformes
Aphyocheirodon hemigrammus	2.51	4.8	SME	Characidae	Characiformes

Aspidoras fuscoguttatus	2.97	3.8	SME	Callichthyidae	Siluriformes
Aspidoras lakoi	2.97	4	SME	Callichthyidae	Siluriformes
Astyanax altiparanae	2.84	10.6	SME	Characidae	Characiformes
Astyanax biotae	2.8	9	SME	Characidae	Characiformes
Astyanax bockmanni	2.8	9	SME	Characidae	Characiformes
Astyanax goyacensis	2.8	9	SME	Characidae	Characiformes
Astyanax paranae	2.8	11.3	SME	Characidae	Characiformes
Astyanax paranahybae	2.8	9	SME	Characidae	Characiformes
Astyanax schubarti	3.14	9	SME	Characidae	Characiformes
Astyanax trierythropterus	2.8	9	SME	Characidae	Characiformes
Brycon nattereri	2.62	29	LM	Characidae	Characiformes
Bryconamericus turiuba	2.66	6.1	SME	Characidae	Characiformes
Bunocephalus larai	3.09	5	SMEP	Aspredinidae	Siluriformes
Cetopsorhamdia iheringi	2.98	10.6	SME	Heptapteridae	Siluriformes
Characidium fasciatum	2.89	6.7	SME	Crenuchidae	Characiformes
Characidium gomesi	3.1	6.5	SME	Crenuchidae	Characiformes
Characidium heirmostigmata	3.09	5.4	SME	Crenuchidae	Characiformes
Characidium oiticicae	3.1	6.8	SME	Crenuchidae	Characiformes
Characidium schubarti	3.25	51.3	SME	Crenuchidae	Characiformes
Characidium xanthopteron	3.08	4.7	SME	Crenuchidae	Characiformes
Chasmocranus brachynema	3.32	13.1	SME	Heptapteridae	Siluriformes
Cichlasoma paranaense	3.33	7.4	SMEP	Cichlidae	Perciformes
Cnesterodon hypselurus	2.97	3.1	SMI	Poeciliidae	Cyprinodontiformes
Coptobrycon bilineatus	3	4.1	SME	Characidae	Characiformes
Corumbataia britskii	2	2.7	SMEP	Loricariidae	Siluriformes
Corumbataia cuestae	2.25	3.3	SMEP	Loricariidae	Siluriformes
Corydoras difluviatilis	2.95	4.7	SME	Callichthyidae	Siluriformes
Corydoras ehrhardti	3.2	4.1	SME	Callichthyidae	Siluriformes
Corydoras flaveolus	2.97	3.4	SME	Callichthyidae	Siluriformes
Corydoras nattereri	2.94	5.4	SME	Callichthyidae	Siluriformes
Creagrutus varii	2.57	4.2	SME	Characidae	Characiformes
Crenicichla britskii	3.14	4.5	SMEP	Cichlidae	Perciformes
Crenicichla haroldoi	3.16	9.8	SMEP	Cichlidae	Perciformes
Crenicichla jaguarensis	3.19	14.8	SMEP	Cichlidae	Perciformes
Crenicichla jupiaensis	3.14	8.2	SMEP	Cichlidae	Perciformes
Cyphocharax nagelii	2	16.3	SME	Curimatidae	Characiformes
Cyphocharax vanderi	2.23	6.8	SME	Curimatidae	Characiformes
Geophagus brasiliensis	2.57	28	SMEP	Cichlidae	Perciformes
Glandulocauda melanopleura	2.94	5.5	SMI	Characidae	Characiformes
Glanidium cesarpintoi	3.32	9.1	SMI	Auchenipteridae	Siluriformes
Gymnotus pantherinus	3.19	13.4	SMEP	Gymnotidae	Gymnotiformes
Gymnotus sylvius	3.14	8.4	SMEP	Gymnotidae	Gymnotiformes
Harttia gracilis	2.52	10.1	SMEP	Loricariidae	Siluriformes
Hasemania crenuchoides	3	6.7	SME	Characidae	Characiformes
Hasemania hanseni	3	3.1	SME	Characidae	Characiformes
Hemigrammus parana	3.01	3.1	SME	Characidae	Characiformes
Heptapterus multiradiatus	3.27	9.6	SME	Heptapteridae	Siluriformes



Hisonotus depressicauda	2	5	SMEP	Loricariidae	Siluriformes
Hisonotus depressinotus	2.36	3	SMEP	Loricariidae	Siluriformes
Hisonotus francirochai	2	3.6	SMEP	Loricariidae	Siluriformes
Hisonotus insperatus	2.35	3	SMEP	Loricariidae	Siluriformes
Hisonotus paulinus	2.05	4	SMEP	Loricariidae	Siluriformes
Hollandichthys multifasciatus	3.03	9.6	SMI	Characidae	Characiformes
Hoplias microcephalus	3.97	35.6	SMEP	Erythrinidae	Characiformes
Hyphessobrycon balbus	2.88	6	SME	Characidae	Characiformes
Hyphessobrycon bifasciatus	2.91	4.7	SME	Characidae	Characiformes
Hyphessobrycon coelestinus	2.96	2.9	SME	Characidae	Characiformes
Hyphessobrycon duragenys	2.87	6.9	SME	Characidae	Characiformes
Hypostomus ancistroides	2	21	SMEP	Loricariidae	Siluriformes
Hypostomus brevis	2.48	7.4	SMEP	Loricariidae	Siluriformes
Hypostomus denticulatus	2.15	19.1	SMEP	Loricariidae	Siluriformes
Hypostomus fluviatilis	2.2	16.5	SMEP	Loricariidae	Siluriformes
Hypostomus heraldoi	2.07	23.6	SMEP	Loricariidae	Siluriformes
Hypostomus hermanni	2.14	24	SMEP	Loricariidae	Siluriformes
Hypostomus iheringi	2.32	11.6	SMEP	Loricariidae	Siluriformes
Hypostomus lexi	2	46	SMEP	Loricariidae	Siluriformes
Hypostomus margaritifer	2.02	33	SMEP	Loricariidae	Siluriformes
Hypostomus meleagris	2	30	SMEP	Loricariidae	Siluriformes
Hypostomus multidens	2.13	19.8	SMEP	Loricariidae	Siluriformes
Hypostomus nigromaculatus	2.36	10.2	SMEP	Loricariidae	Siluriformes
Hypostomus paulinus	2.28	13.1	SMEP	Loricariidae	Siluriformes
Hypostomus scaphycephs	2.74	3.5	SMEP	Loricariidae	Siluriformes
Hypostomus strigaticeps	2.23	15	SMEP	Loricariidae	Siluriformes
Hypostomus tietensis	2.29	12.5	SMEP	Loricariidae	Siluriformes
Hypostomus topavae	2	70	SMEP	Loricariidae	Siluriformes
Hypostomus variipictus	2	37	SMEP	Loricariidae	Siluriformes
Imparfinis borodini	2.97	15.7	SME	Heptapteridae	Siluriformes
Imparfinis mirini	2.98	8.5	SME	Heptapteridae	Siluriformes
Imparfinis schubarti	2.98	9.3	SME	Heptapteridae	Siluriformes
Isbrueckerichthys calvus	2.36	9	SMEP	Loricariidae	Siluriformes
Isbrueckerichthys saxicola	2.37	8.8	SMEP	Loricariidae	Siluriformes
Kolpotocheiroidon theloura	2.66	3	SMI	Characidae	Characiformes
Leporinus aguapeiensis	2.17	18.8	SME	Anostomidae	Characiformes
Leporinus amblyrhynchus	2.16	19.6	SME	Anostomidae	Characiformes
Leporinus microphthalmus	2.33	11.8	SME	Anostomidae	Characiformes
Leporinus paranensis	2.23	16	SME	Anostomidae	Characiformes
Leporinus tigrinus	2.14	25	SME	Anostomidae	Characiformes
Lophiobrycon weitzmani	3.27	2.9	SMI	Characidae	Characiformes
Loricaria lentiginosa	2.09	51.4	SMEP	Loricariidae	Siluriformes
Loricaria piracicabae	2.38	17	SMEP	Loricariidae	Siluriformes
Microglanis garavelloi	3.39	4.2	SMEP	Pseudopimelodidae	Siluriformes
Microlepidogaster longiculla	2	5	SMEP	Loricariidae	Siluriformes
Microlepidogaster perforatus	2	5	SMEP	Loricariidae	Siluriformes
Mimagoniates microlepis	3.2	6.1	SMI	Characidae	Characiformes

Moenkhausia forestii	3	3.8	SME	Characidae	Characiformes
Neoplecostomus corumba	2.41	7.8	SMEP	Loricariidae	Siluriformes
Neoplecostomus paranensis	2.35	9.3	SMEP	Loricariidae	Siluriformes
Neoplecostomus selene	2.31	10.2	SMEP	Loricariidae	Siluriformes
Neoplecostomus yapo	2.28	11	SMEP	Loricariidae	Siluriformes
Odontostilbe stenodon	2.63	3.3	SME	Characidae	Characiformes
Oligosarcus pintoii	3.45	8.4	SME	Characidae	Characiformes
Oligosarcus planaltinae	3.64	9.9	SME	Characidae	Characiformes
Otothyropsis marapoama	2	3.8	SMEP	Loricariidae	Siluriformes
Pamphorichthys hollandi	2.99	2.5	SMI	Poeciliidae	Cyprinodontiformes
Parastegophilus paulensis	3.18	5.4	SME	Trichomycteridae	Siluriformes
Pareorhina carrancas	2.65	4.1	SMEP	Loricariidae	Siluriformes
Parodon moreirai	2.32	11.8	SME	Parodontidae	Characiformes
Phalloceros reisi	2.95	2.7	SMI	Poeciliidae	Cyprinodontiformes
Phallotorynus fasciolatus	2.98	2.5	SMI	Poeciliidae	Cyprinodontiformes
Phallotorynus jucundus	2.98	2.5	SMI	Poeciliidae	Cyprinodontiformes
Phallotorynus pankalos	2.98	2.8	SMI	Poeciliidae	Cyprinodontiformes
Phenacorhamdia tenebrosa	3.22	6.7	SME	Heptapteridae	Siluriformes
Phenacorhamdia unifasciata	3.2	6.2	SME	Heptapteridae	Siluriformes
Piabina anhembi	3	6.5	SME	Characidae	Characiformes
Pimelodella avanhandavae	3.46	9.6	SME	Heptapteridae	Siluriformes
Pimelodella boschmai	3.53	10	SME	Heptapteridae	Siluriformes
Pimelodella meeki	3.48	10.2	SME	Heptapteridae	Siluriformes
Pimelodella rudolphi	3.55	10.5	SME	Heptapteridae	Siluriformes
Pimelodus heraldoi	3.26	18	SME	Pimelodidae	Siluriformes
Pimelodus paranaensis	3.28	23.1	SME	Pimelodidae	Siluriformes
Pimelodus platicirris	3.28	16	SME	Pimelodidae	Siluriformes
Planaltina britskii	3.23	4.5	SMI	Characidae	Characiformes
Planaltina glandipedis	3.23	4.5	SMI	Characidae	Characiformes
Planaltina myersi	3.23	4.6	SMI	Characidae	Characiformes
Prochilodus vimboides	2.04	33	LM	Prochilodontidae	Characiformes
Proloricaria prolixa	3	35	SMEP	Loricariidae	Siluriformes
Pseudocorynopoma heterandria	3.28	5.6	SMI	Characidae	Characiformes
Pseudopimelodus aff. pulcher	3.39	8.7	SMEP	Pimelodidae	Siluriformes
Pseudotocinclus tietensis	2	6	SMEP	Loricariidae	Siluriformes
Rhamdella longipinnis	3.26	8.8	SME	Heptapteridae	Siluriformes
Rhamdiopsis microcephala	3.24	7.8	SME	Heptapteridae	Siluriformes
Rhinelepis aspera	2.08	33	LM	Loricariidae	Siluriformes
Rineloricaria latirostris	2.23	36	SMEP	Loricariidae	Siluriformes
Rineloricaria pentamaculata	2.44	10	SMEP	Loricariidae	Siluriformes
Rivulus apiamici	3.12	3	SME	Rivulidae	Cyprinodontiformes
Rivulus egens	3.21	3.3	SME	Rivulidae	Cyprinodontiformes
Rivulus faucireticulatus	3.12	3	SME	Rivulidae	Cyprinodontiformes
Rivulus formosensis	3.15	3.3	SME	Rivulidae	Cyprinodontiformes
Rivulus giarettai	3.17	3.2	SME	Rivulidae	Cyprinodontiformes
Rivulus illuminatus	3.14	2.9	SME	Rivulidae	Cyprinodontiformes
Rivulus pictus	3.19	5	SME	Rivulidae	Cyprinodontiformes

Rivulus pinima	3.12	3	SME	Rivulidae	Cyprinodontiformes
Rivulus rossoi	3.21	3.5	SME	Rivulidae	Cyprinodontiformes
Rivulus rutilicaudus	3.21	3.5	SME	Rivulidae	Cyprinodontiformes
Rivulus scalaris	3.21	3.5	SME	Rivulidae	Cyprinodontiformes
Rivulus vittatus	3.21	3.5	SME	Rivulidae	Cyprinodontiformes
Roeboides microlepis	4.03	20	SME	Characidae	Characiformes
Salminus hilarii	3	50	LM	Characidae	Characiformes
Schizodon altoparanae	2.49	23	SME	Anostomidae	Characiformes
Schizodon intermedius	2.45	28.7	SME	Anostomidae	Characiformes
Scleromystax macropterus	2.94	8.7	SME	Callichthyidae	Siluriformes
Serrapinnus heterodon	2.49	4.1	SME	Characidae	Characiformes
Serrapinnus notomelas	2.21	3.6	SME	Characidae	Characiformes
Simpsonichthys boitonei	3.17	5.5	SME	Rivulidae	Cyprinodontiformes
Simpsonichthys nigromaculatus	3.08	2.6	SME	Rivulidae	Cyprinodontiformes
Simpsonichthys parallelus	3.05	2.3	SME	Rivulidae	Cyprinodontiformes
Simpsonichthys santanae	3.07	3	SME	Rivulidae	Cyprinodontiformes
Spintherobolus papilliferus	2.27	6.1	SME	Characidae	Characiformes
Steindachneridion punctatum	4.25	69.7	LM	Pimelodidae	Siluriformes
Steindachneridion scriptum	4.27	90	LM	Pimelodidae	Siluriformes
Steindachnerina corumbae	2	11.7	SME	Curimatidae	Characiformes
Steindachnerina insculpta	2.07	10.6	SME	Curimatidae	Characiformes
Sternarchella curvioperculata	3.29	25.3	SME	Apteronotidae	Gymnotiformes
Sternarchorhynchus britskii	3.3	26.1	SME	Apteronotidae	Gymnotiformes
Sternopygus macrurus	3.22	141	SMEP	Sternopygidae	Gymnotiformes
Tatia neivai	3.28	8.2	SMI	Auchenipteridae	Siluriformes
Taunaya bifasciata	3.33	14	SMEP	Loricariidae	Siluriformes
Tembeassu marauna	3.26	19.6	SME	Apteronotidae	Gymnotiformes
Trachelyopterus coriaceus	3.43	18	SMI	Auchenipteridae	Siluriformes
Trichomycterus candidus	3.2	7.5	SME	Trichomycteridae	Siluriformes
Trichomycterus diabolus	3.2	6.1	SME	Trichomycteridae	Siluriformes
Trichomycterus maracaya	3.27	5.1	SME	Trichomycteridae	Siluriformes
Trichomycterus paolence	3.2	6.8	SME	Trichomycteridae	Siluriformes
Trichomycterus pauciradiatus	3.14	5.2	SME	Trichomycteridae	Siluriformes

Fauna of Lower Paraná Ecoregion - Potential invader donor pool

Species	Trophic_level	Size	Reproduction	Family	Order
<i>Ageneiosus militaris</i>	3.76	30	SMI	Auchenipteridae	Siluriformes
<i>Ancistrus cirrhosus</i>	2	8.9	SMEP	Loricariidae	Siluriformes
<i>Apareiodon affinis</i>	2.21	14.3	SME	Parodontidae	Characiformes
<i>Aphyocharax anisitsi</i>	3.22	5.5	SME	Characidae	Characiformes
<i>Aphyocharax dentatus</i>	3.02	7.2	SME	Characidae	Characiformes
<i>Astyanax eigenmanniorum</i>	2.86	4.9	SME	Characidae	Characiformes
<i>Astyanax fasciatus</i>	2.75	16.8	SME	Characidae	Characiformes
<i>Auchenipterus osteomystax</i>	3.6	27	SMI	Auchenipteridae	Siluriformes
<i>Australoheros facetus</i>	3.33	19.3	SMEP	Cichlidae	Perciformes
<i>Brycon orbignyanus</i>	2.51	79	LM	Characidae	Characiformes

<i>Bryconamericus iheringii</i>	2	11	SME	Characidae	Characiformes
<i>Bryconamericus stramineus</i>	2.73	11.4	SME	Characidae	Characiformes
<i>Callichthys callichthys</i>	2.95	17	SME	Callichthyidae	Siluriformes
<i>Cetopsis gobioides</i>	3.64	10.9	SME	Cetopsidae	Siluriformes
<i>Characidium zebra</i>	3.2	6.5	SME	Crenuchidae	Characiformes
<i>Corydoras aeneus</i>	2.96	7.5	SME	Callichthyidae	Siluriformes
<i>Corydoras paleatus</i>	2.94	5.9	SME	Callichthyidae	Siluriformes
<i>Crenicichla niederleini</i>	3.23	23.5	SMEP	Cichlidae	Perciformes
<i>Cyphocharax modestus</i>	2	16.2	SME	Curimatidae	Characiformes
<i>Eigenmannia trilineata</i>	3.05	25	SME	Sternopygidae	Gymnotiformes
<i>Eigenmannia virescens</i>	3	35.8	SME	Sternopygidae	Gymnotiformes
<i>Galeocharax knerii</i>	3.96	22	SME	Characidae	Characiformes
<i>Gymnogeophagus australis</i>	3.34	15.5	SMEP	Cichlidae	Perciformes
<i>Gymnogeophagus setequedas</i>	3.3	9.8	SMEP	Cichlidae	Perciformes
<i>Gymnotus carapo</i>	2.99	76	SMEP	Gymnotidae	Gymnotiformes
<i>Hemigrammus marginatus</i>	2.81	4.5	SME	Characidae	Characiformes
<i>Hemisorubim platyrhynchos</i>	4.5	52.5	LM	Pimelodidae	Siluriformes
<i>Hoplias aff. malabaricus</i>	4.5	55.2	SMEP	Erythrinidae	Characiformes
<i>Hoplosternum littorale</i>	2.68	24	SME	Callichthyidae	Siluriformes
<i>Hyphessobrycon anisitsi</i>	2.98	6	SME	Characidae	Characiformes
<i>Hyphessobrycon eques</i>	3.06	4	SME	Characidae	Characiformes
<i>Hyphessobrycon reticulatus</i>	2.88	4.9	SME	Characidae	Characiformes
<i>Hypostomus albopunctatus</i>	2.03	27	SMEP	Loricariidae	Siluriformes
<i>Hypostomus regani</i>	2	39.7	SMEP	Loricariidae	Siluriformes
<i>Iheringichthys labrosus</i>	2.94	29.7	SME	Pimelodidae	Siluriformes
<i>Leporellus vittatus</i>	2.25	30	SME	Anostomidae	Characiformes
<i>Leporinus elongatus</i>	2	39.8	LM	Anostomidae	Characiformes
<i>Leporinus friderici</i>	3.26	40	SME	Anostomidae	Characiformes
<i>Leporinus lacustris</i>	3.72	20.3	SME	Anostomidae	Characiformes
<i>Leporinus obtusidens</i>	2	76	LM	Anostomidae	Characiformes
<i>Leporinus octofasciatus</i>	2	23.5	SME	Anostomidae	Characiformes
<i>Leporinus striatus</i>	2	25	SME	Anostomidae	Characiformes
<i>Lepthoplosternum pectorale</i>	2.92	6	SME	Callichthyidae	Siluriformes
<i>Megalancistrus parananus</i>	2	58.8	SMEP	Loricariidae	Siluriformes
<i>Megalonema platanum</i>	3.95	40	SME	Pimelodidae	Siluriformes
<i>Moenkhausia intermedia</i>	2.65	8	SME	Characidae	Characiformes
<i>Moenkhausia sanctaefilomenae</i>	2.95	7	SME	Characidae	Characiformes
<i>Myleus tiete</i>	2.16	15.2	LM	Characidae	Characiformes
<i>Mylossoma duriventre</i>	2.84	25	LM	Characidae	Characiformes
<i>Odontostilbe microcephala</i>	2.42	4.6	SME	Characidae	Characiformes
<i>Oligosarcus paranensis</i>	3.89	20.5	SME	Characidae	Characiformes
<i>Paravandellia oxyptera</i>	3.08	2.8	SME	Trichomycteridae	Siluriformes
<i>Parodon nasus</i>	2.3	12.7	SME	Parodontidae	Characiformes
<i>Phalloceros harpagos</i>	2.5	3.4	SMI	Poeciliidae	Cyprinodontiformes
<i>Phallotorynus victoriae</i>	2.98	2.3	SMI	Poeciliidae	Cyprinodontiformes
<i>Piabina argentea</i>	3	6.8	SME	Characidae	Characiformes
<i>Piaractus mesopotamicus</i>	2	40.5	LM	Characidae	Characiformes

<i>Pimelodella gracilis</i>	3.24	18	SME	Heptapteridae	Siluriformes
<i>Pimelodus maculatus</i>	2.87	51	SME	Pimelodidae	Siluriformes
<i>Pinirampus pirinampu</i>	4.5	120	LM	Pimelodidae	Siluriformes
<i>Poecilia vivipara</i>	3.2	4	SMI	Poeciliidae	Cyprinodontiformes
<i>Prochilodus lineatus</i>	2.18	80	LM	Prochilodontidae	Characiformes
<i>Pseudopimelodus mangurus</i>	3.93	69	SMEP	Pimelodidae	Siluriformes
<i>Pseudoplatystoma corruscans</i>	4.5	166	LM	Pimelodidae	Siluriformes
<i>Pseudoplatystoma fasciatum</i>	4.38	104	LM	Pimelodidae	Siluriformes
<i>Pterygoplichthys anisitsi</i>	2.06	42	SMEP	Loricariidae	Siluriformes
<i>Pygocentrus nattereri</i>	3.72	50	SMEP	Characidae	Characiformes
<i>Pyrrhulina australis</i>	3.23	5	SME	Lebiasinidae	Characiformes
<i>Rhamdia quelen</i>	3.16	47.4	SME	Heptapteridae	Siluriformes
<i>Rhaphiodon vulpinus</i>	4.5	80	LM	Cynodontidae	Characiformes
<i>Rhinodoras dorbignyi</i>	2.69	50	SME	Doradidae	Siluriformes
<i>Salminus brasiliensis</i>	3.79	100	LM	Characidae	Characiformes
<i>Schizodon borellii</i>	2.45	30	SME	Anostomidae	Characiformes
<i>Schizodon nasutus</i>	2.83	40.2	SME	Anostomidae	Characiformes
<i>Serrasalmus maculatus</i>	4.07	26	SMEP	Characidae	Characiformes
<i>Synbranchus marmoratus</i>	2.76	150	SME	Synbranchidae	Synbranchiformes
<i>Zungaro jahu</i>	4.48	140	LM	Pimelodidae	Siluriformes
<i>Acestrorhynchus pantaneiro</i>	4.23	35.2	SME	Acestrorhynchidae	Characiformes
<i>Ageneiosus inermis</i>	3.98	59	SMI	Auchenipteridae	Siluriformes
<i>Ageneiosus ucayalensis</i>	3.66	29	SMI	Auchenipteridae	Siluriformes
<i>Apteronotus albifrons</i>	3.03	50	SME	Apteronotidae	Gymnotiformes
<i>Apteronotus caudimaculosus</i>	3.31	28.7	SME	Apteronotidae	Gymnotiformes
<i>Apteronotus ellisi</i>	3.32	32.8	SME	Apteronotidae	Gymnotiformes
<i>Brachyhypopomus gauderio</i>	3	14.9	SME	Hypopomidae	Gymnotiformes
<i>Bryconamericus exodon</i>	2.73	5.7	SME	Characidae	Characiformes
<i>Catathyridium jenynsii</i>	3.31	23	SME	Achiridae	Pleuronectiformes
<i>Characidium laterale</i>	3.1	3.5	SME	Crenuchidae	Characiformes
<i>Cynopotamus kincaidi</i>	3.95	25.8	SME	Characidae	Characiformes
<i>Cyphocharax gillii</i>	2	10	SME	Curimatidae	Characiformes
<i>Doras eigenmanni</i>	2.83	10	SME	Doradidae	Siluriformes
<i>Erythrinus erythrinus</i>	3.73	20	SMEP	Erythrinidae	Characiformes
<i>Farlowella hahni</i>	2.34	20.1	SMEP	Loricariidae	Siluriformes
<i>Gymnorhamphichthys hypostomus</i>	3.15	21.5	SME	Rhamphichthyidae	Gymnotiformes
<i>Gymnotus inaequilabiatus</i>	3.25	30	SMEP	Gymnotidae	Gymnotiformes
<i>Gymnotus pantanal</i>	3.27	25.1	SMEP	Gymnotidae	Gymnotiformes
<i>Gymnotus paraguensis</i>	3.24	24	SMEP	Gymnotidae	Gymnotiformes
<i>Hemiodus orthonops</i>	2.66	25	SME	Hemiodontidae	Characiformes
<i>Heptapterus mustelinus</i>	3.39	20.9	SME	Heptapteridae	Siluriformes
<i>Hoplerethrinus unitaeniatus</i>	3.41	25	SMEP	Erythrinidae	Characiformes
<i>Hypophthalmus edentatus</i>	2.91	57.5	SME	Pimelodidae	Siluriformes
<i>Hypostomus cochliodon</i>	2.08	23	SMEP	Loricariidae	Siluriformes
<i>Hypostomus commersoni</i>	2	60.5	SMEP	Loricariidae	Siluriformes
<i>Hypostomus dlouhyi</i>	2.06	24.5	SMEP	Loricariidae	Siluriformes
<i>Hypostomus microstomus</i>	2.07	24	SMEP	Loricariidae	Siluriformes

<i>Hypostomus ternetzi</i>	2.01	34.3	SMEP	Loricariidae	Siluriformes
<i>Knodus moenkhausii</i>	2.62	4.5	SME	Characidae	Characiformes
<i>Leporinus macrocephalus</i>	2	60	LM	Anostomidae	Characiformes
<i>Loricaria simillima</i>	2.37	18	SMEP	Loricariidae	Siluriformes
<i>Loricariichthys platymetopon</i>	2.45	30	SMEP	Loricariidae	Siluriformes
<i>Loricariichthys rostratus</i>	2.55	27.5	SMEP	Loricariidae	Siluriformes
<i>Megalechis thoracata</i>	2.88	12.4	SME	Callichthyidae	Siluriformes
<i>Metynnis maculatus</i>	2.9	18	SME	Characidae	Characiformes
<i>Metynnis mola</i>	2.89	15	SME	Characidae	Characiformes
<i>Odontesthes bonariensis</i>	2.57	50	SME	Atherinopsidae	Atheriniformes
<i>Oxydoras eigenmanni</i>	2.83	10	SME	Doradidae	Siluriformes
<i>Pimelodella taenioptera</i>	3.56	12.1	SME	Heptapteridae	Siluriformes
<i>Pimelodus ornatus</i>	3.34	38.5	SME	Pimelodidae	Siluriformes
<i>Platydoras armatulus</i>	2.76	20	SME	Doradidae	Siluriformes
<i>Potamotrygon falkneri</i>	3.2	47	SMI	Potamotrygonidae	Myliobatiformes
<i>Potamotrygon motoro</i>	3.2	50	SMI	Potamotrygonidae	Myliobatiformes
<i>Psellogrammus kennedyi</i>	3	5.9	SME	Characidae	Characiformes
<i>Pterodoras granulosus</i>	2.55	70	LM	Doradidae	Siluriformes
<i>Rhamphichthys hahni</i>	3.16	26.7	SME	Rhamphichthyidae	Gymnotiformes
<i>Roeboides descalvadensis</i>	3.73	8.9	SME	Characidae	Characiformes
<i>Serrasalmus marginatus</i>	3.55	27	SMEP	Characidae	Characiformes
<i>Sorubim lima</i>	4.09	54.2	SMEP	Pimelodidae	Siluriformes
<i>Steindachnerina brevipinna</i>	2	20.5	SME	Curimatidae	Characiformes
<i>Trachelyopterus galeatus</i>	3.14	22	SMI	Auchenipteridae	Siluriformes
<i>Trachydoras paraguayensis</i>	2.66	10.4	SME	Doradidae	Siluriformes
<i>Triporthus nematurus</i>	2.8	18.3	SME	Characidae	Characiformes
<i>Abramites hypselonotus</i>	2.93	14	SME	Anostomidae	Characiformes
<i>Aequidens plagiazonatus</i>	3.19	10.3	SMEP	Cichlidae	Perciformes
<i>Amaralia cf. hypsiura</i>	3.17	13.3	SMEP	Aspredinidae	Siluriformes
<i>Anadoras weddellii</i>	2.81	15	SME	Doradidae	Siluriformes
<i>Ancistrus dubius</i>	2	12.6	SMEP	Loricariidae	Siluriformes
<i>Ancistrus piriformis</i>	2.16	8.3	SMEP	Loricariidae	Siluriformes
<i>Apistogramma borellii</i>	3.26	3.9	SMEP	Cichlidae	Perciformes
<i>Apistogramma commbrae</i>	3.17	3.3	SMEP	Cichlidae	Perciformes
<i>Apistogramma inconspicua</i>	3.29	3.8	SMEP	Cichlidae	Perciformes
<i>Apistogramma trifasciata</i>	3.29	3.8	SMEP	Cichlidae	Perciformes
<i>Astyanax abramis</i>	2.76	14	SME	Characidae	Characiformes
<i>Astyanax asuncionensis</i>	2.83	15	SME	Characidae	Characiformes
<i>Astyanax bimaculatus</i>	2.17	17.5	SME	Characidae	Characiformes
<i>Astyanax correntinus</i>	2.8	9	SME	Characidae	Characiformes
<i>Astyanax leonidas</i>	2.87	4.6	SME	Characidae	Characiformes
<i>Astyanax scabripinnis</i>	2.88	7.8	SME	Characidae	Characiformes
<i>Astyanax troya</i>	2.81	7.4	SME	Characidae	Characiformes
<i>Astyanax tupi</i>	2.81	7.3	SME	Characidae	Characiformes
<i>Auchenipterus nigripinnis</i>	3.57	20.2	SMI	Auchenipteridae	Siluriformes
<i>Austroloheros guarani</i>	3.18	12.9	SMEP	Cichlidae	Perciformes
<i>Austrolebias bellottii</i>	3.26	7	SME	Rivulidae	Cyprinodontiformes

<i>Austrolebias nigripinnis</i>	3.12	7	SME	Rivulidae	Cyprinodontiformes
<i>Austrolebias paranaensis</i>	3.16	7	SME	Rivulidae	Cyprinodontiformes
<i>Bergiaria platana</i>	3.57	9.1	SME	Pimelodidae	Siluriformes
<i>Bergiaria westermanni</i>	3.57	9.1	SME	Pimelodidae	Siluriformes
<i>Brachyhypopomus brevirostris</i>	3.2	34.7	SME	Hypopomidae	Gymnotiformes
<i>Bryconamericus agna</i>	2.64	6.5	SME	Characidae	Characiformes
<i>Bryconamericus eigenmanni</i>	2.66	6.1	SME	Characidae	Characiformes
<i>Bryconamericus mennii</i>	2.69	11.4	SME	Characidae	Characiformes
<i>Bryconamericus rubropictus</i>	2.66	11.4	SME	Characidae	Characiformes
<i>Bujurquina vittata</i>	3.38	9	SMEP	Cichlidae	Perciformes
<i>Bunocephalus doriae</i>	3.13	8.3	SMEP	Aspredinidae	Siluriformes
<i>Chaetobranchopsis australis</i>	3.5	12	SMEP	Cichlidae	Perciformes
<i>Characidium etzeli</i>	3.09	5.6	SME	Crenuchidae	Characiformes
<i>Characidium occidentale</i>	3.08	4.8	SME	Crenuchidae	Characiformes
<i>Characidium rachovii</i>	3.07	4.3	SME	Crenuchidae	Characiformes
<i>Charax leticiae</i>	3.7	10	SME	Characidae	Characiformes
<i>Cheirodon interruptus</i>	2.39	5.8	SME	Characidae	Characiformes
<i>Cichlasoma dimerus</i>	3.44	11.7	SMEP	Cichlidae	Perciformes
<i>Cichlasoma pusillum</i>	3.31	6.6	SMEP	Cichlidae	Perciformes
<i>Clupeacharax anchoveoides</i>	3.02	6.6	SME	Characidae	Characiformes
<i>Cnesterodon raddai</i>	2.98	2.3	SMI	Poeciliidae	Cyprinodontiformes
<i>Corydoras diphys</i>	2.95	4.5	SME	Callichthyidae	Siluriformes
<i>Corydoras ellisae</i>	2.95	5	SME	Callichthyidae	Siluriformes
<i>Corydoras hastatus</i>	2.98	2.4	SME	Callichthyidae	Siluriformes
<i>Corydoras micracanthus</i>	2.96	4	SME	Callichthyidae	Siluriformes
<i>Corydoras undulatus</i>	2.95	4.4	SME	Callichthyidae	Siluriformes
<i>Crenicichla lepidota</i>	3.56	18	SMEP	Cichlidae	Perciformes
<i>Crenicichla mandelburgeri</i>	3.17	11.5	SMEP	Cichlidae	Perciformes
<i>Crenicichla semifasciata</i>	3.2	15	SMEP	Cichlidae	Perciformes
<i>Crenicichla vittata</i>	3.24	26	SMEP	Cichlidae	Perciformes
<i>Curimatella dorsalis</i>	2.15	11.4	SME	Curimatidae	Characiformes
<i>Cynopotamus argenteus</i>	3.95	24	SME	Characidae	Characiformes
<i>Cyphocharax platanus</i>	2	13.4	SME	Curimatidae	Characiformes
<i>Cyphocharax spilatus</i>	2.08	8.9	SME	Curimatidae	Characiformes
<i>Cyphocharax voga</i>	2	19.6	SME	Curimatidae	Characiformes
<i>Diapoma terofali</i>	3.24	4.8	SMI	Characidae	Characiformes
<i>Galeocharax humeralis</i>	4.01	30.5	SME	Characidae	Characiformes
<i>Gymnogeophagus balzanii</i>	3.33	12	SMEP	Cichlidae	Perciformes
<i>Gymnogeophagus che</i>	3.33	11.6	SMEP	Cichlidae	Perciformes
<i>Gymnogeophagus meridionalis</i>	3.28	8.8	SMEP	Cichlidae	Perciformes
<i>Hemiodus semitaeniatus</i>	2.71	20	SME	Hemiodontidae	Characiformes
<i>Hisonotus maculipinnis</i>	2.05	4	SMEP	Loricariidae	Siluriformes
<i>Hisonotus nigricauda</i>	2	5	SMEP	Loricariidae	Siluriformes
<i>Homodiaetus anisitsi</i>	3.14	4.2	SME	Trichomycteridae	Siluriformes
<i>Hyphessobrycon arianae</i>	2.96	2.4	SME	Characidae	Characiformes
<i>Hyphessobrycon elachys</i>	2.99	2	SME	Characidae	Characiformes
<i>Hyphessobrycon guarani</i>	2.93	3.1	SME	Characidae	Characiformes



<i>Hyphessobrycon igneus</i>	2.92	3.4	SME	Characidae	Characiformes
<i>Hyphessobrycon meridionalis</i>	2.98	4.6	SME	Characidae	Characiformes
<i>Hyphessobrycon wajati</i>	2.93	3.1	SME	Characidae	Characiformes
<i>Hypophthalmus oremaculatus</i>	3.4	50	SME	Pimelodidae	Siluriformes
<i>Hypoptopoma inexpectatum</i>	2	7.1	SMEP	Loricariidae	Siluriformes
<i>Hypostomus alatus</i>	2.03	27	SMEP	Loricariidae	Siluriformes
<i>Hypostomus auroguttatus</i>	2.07	28.6	SMEP	Loricariidae	Siluriformes
<i>Hypostomus boulengeri</i>	2.06	24.5	SMEP	Loricariidae	Siluriformes
<i>Hypostomus luteomaculatus</i>	2.01	28	SMEP	Loricariidae	Siluriformes
<i>Hypostomus piratatu</i>	2.02	27.5	SMEP	Loricariidae	Siluriformes
<i>Hypostomus variostictus</i>	2.64	5.7	SMEP	Loricariidae	Siluriformes
<i>Imparfinis mishky</i>	2.98	8.5	SME	Heptapteridae	Siluriformes
<i>Ituglanis eichorniarum</i>	3.17	5	SME	Trichomycteridae	Siluriformes
<i>Jenynsia multidentata</i>	2.9	6.56	SMI	Anablepidae	Cyprinodontiformes
<i>Laetacara dorsigera</i>	3.09	6	SMEP	Cichlidae	Perciformes
<i>Lepidosiren paradoxa</i>	3.11	125	SMEP	Lepidosirenidae	Lepidosireniformes
<i>Leporinus acutidens</i>	2.05	33	SME	Anostomidae	Characiformes
<i>Loricaria apeltogaster</i>	2.27	26	SMEP	Loricariidae	Siluriformes
<i>Loricariichthys anus</i>	2.59	46	SMEP	Loricariidae	Siluriformes
<i>Loricariichthys labialis</i>	2.59	22	SMEP	Loricariidae	Siluriformes
<i>Loricariichthys melanocheilus</i>	2.6	20.9	SMEP	Loricariidae	Siluriformes
<i>Luciopimelodus pati</i>	4.31	103	SME	Pimelodidae	Siluriformes
<i>Markiana nigripinnis</i>	3	10.4	SME	Characidae	Characiformes
<i>Megalebias elongatus</i>	3.41	22	SME	Rivulidae	Cyprinodontiformes
<i>Megalonema argentina</i>	3.93	27.1	SME	Pimelodidae	Siluriformes
<i>Megalonema pauciradiatum</i>	3.28	3.8	SME	Pimelodidae	Siluriformes
<i>Mesonauta festivus</i>	2.51	8.2	SMEP	Cichlidae	Perciformes
<i>Microglanis parahybae</i>	3.47	8	SMEP	Pseudopimelodidae	Siluriformes
<i>Moenkhausia dichroua</i>	3.45	10	SME	Characidae	Characiformes
<i>Myleus levis</i>	2	20	LM	Characidae	Characiformes
<i>Odontostilbe paraguayensis</i>	2.55	4	SME	Characidae	Characiformes
<i>Odontostilbe pequirã</i>	2.44	5.6	SME	Characidae	Characiformes
<i>Oligosarcus jenynsii</i>	3.97	31	SME	Characidae	Characiformes
<i>Oligosarcus menezesi</i>	3.75	13.8	SME	Characidae	Characiformes
<i>Oligosarcus oligolepis</i>	3.15	2.5	SME	Characidae	Characiformes
<i>Otocinclus flexilis</i>	2	5.5	SMEP	Loricariidae	Siluriformes
<i>Otocinclus mimulus</i>	2	4.3	SMEP	Loricariidae	Siluriformes
<i>Otocinclus vestitus</i>	2.29	3.2	SMEP	Loricariidae	Siluriformes
<i>Otocinclus vittatus</i>	2.47	3.3	SMEP	Loricariidae	Siluriformes
<i>Oxydoras kneri</i>	3.17	70	SME	Doradidae	Siluriformes
<i>Pachyrurus bonariensis</i>	3.51	22.6	SME	Sciaenidae	Perciformes
<i>Paraloricaria agastor</i>	2.5	10.8	SMEP	Loricariidae	Siluriformes
<i>Paraloricaria vetula</i>	2.12	55.4	SMEP	Loricariidae	Siluriformes
<i>Parapimelodus valenciennis</i>	3.7	17	SME	Pimelodidae	Siluriformes
<i>Parastegophilus maculatus</i>	4.2	6	SME	Trichomycteridae	Siluriformes
<i>Pellona flavipinnis</i>	4.5	73	SME	Pristigasteridae	Characiformes
<i>Phalloceros caudimaculatus</i>	2.82	3.5	SMI	Poeciliidae	Cyprinodontiformes



<i>Phallotorynus dispilos</i>	2.98	1.8	SMI	Poeciliidae	Cyprinodontiformes
<i>Pimelodella howesi</i>	3.46	7.9	SME	Heptapteridae	Siluriformes
<i>Pimelodus absconditus</i>	3.48	28.7	SME	Pimelodidae	Siluriformes
<i>Pimelodus albicans</i>	3.36	57	SME	Pimelodidae	Siluriformes
<i>Pimelodus argenteus</i>	3.27	25	SME	Pimelodidae	Siluriformes
<i>Pimelodus brevis</i>	3.31	28.5	SME	Pimelodidae	Siluriformes
<i>Pimelodus mystriosus</i>	3.24	14.3	SME	Pimelodidae	Siluriformes
<i>Plagioscion ternetzi</i>	3.92	39	SME	Sciaenidae	Perciformes
<i>Platydoras costatus</i>	3.04	24	SME	Doradidae	Siluriformes
<i>Poptella paraguayensis</i>	3.22	7	SME	Characidae	Characiformes
<i>Potamorhina squamoraievis</i>	2.02	23.4	SME	Curimatidae	Characiformes
<i>Potamorrhaphis eigenmanni</i>	3.9	22.8	SME	Belonidae	Beloniformes
<i>Potamotrygon brachyura</i>	3.2	95	SMI	Potamotrygonidae	Myliobatiformes
<i>Potamotrygon castexi</i>	3.2	60	SMI	Potamotrygonidae	Myliobatiformes
<i>Potamotrygon hystrix</i>	3.2	40	SMI	Potamotrygonidae	Myliobatiformes
<i>Potamotrygon schuhmacheri</i>	3.2	25	SMI	Potamotrygonidae	Myliobatiformes
<i>Prionobrama paraguayensis</i>	3	5	SME	Characidae	Characiformes
<i>Psectrogaster curviventris</i>	2	17.1	SME	Curimatidae	Characiformes
<i>Pseudobunocephalus iheringii</i>	3.1	5.9	SMEP	Aspredinidae	Siluriformes
<i>Pseudobunocephalus rugosus</i>	3.05	3	SMEP	Aspredinidae	Siluriformes
<i>Pseudocorynopoma doriae</i>	3.3	6.2	SMI	Characidae	Characiformes
<i>Pseudohemiodon laticeps</i>	2.23	29.8	SMEP	Loricariidae	Siluriformes
<i>Pseudotyloturus angusticeps</i>	3.99	29.8	SME	Belonidae	Beloniformes
<i>Ramnogaster melanostoma</i>	3.2	10	SME	Clupeidae	Clupeiformes
<i>Rhamdella cainguae</i>	3.35	15.8	SME	Heptapteridae	Siluriformes
<i>Rhinelepis strigosa</i>	2	40	LM	Loricariidae	Siluriformes
<i>Ricola macrops</i>	2.32	21	SMEP	Loricariidae	Siluriformes
<i>Rineloricaria microlepidogaster</i>	2.35	19.3	SMEP	Loricariidae	Siluriformes
<i>Rineloricaria misionera</i>	2.53	9.74	SMEP	Loricariidae	Siluriformes
<i>Rivulus punctatus</i>	3.11	3.5	SME	Rivulidae	Cyprinodontiformes
<i>Roeboides prognathus</i>	4.11	14	SME	Characidae	Characiformes
<i>Schizodon isognathus</i>	2.48	35	SME	Anostomidae	Characiformes
<i>Schizodon platae</i>	2.45	30	SME	Anostomidae	Characiformes
<i>Serrapinnus calliurus</i>	2.62	4.4	SME	Characidae	Characiformes
<i>Spatuloricaria evansii</i>	2.34	20	SMEP	Loricariidae	Siluriformes
<i>Steindachnerina biornata</i>	2	18.8	SME	Curimatidae	Characiformes
<i>Steindachnerina conspersa</i>	2	12.8	SME	Curimatidae	Characiformes
<i>Sturisoma barbatum</i>	2.25	28	SMEP	Loricariidae	Siluriformes
<i>Tetragonopterus argenteus</i>	3.03	11.2	SME	Characidae	Characiformes
<i>Thoracocharax stellatus</i>	3.46	6.7	SME	Gasteropelecidae	Characiformes
<i>Trachelyopterus striatulus</i>	3.46	20	SMI	Auchenipteridae	Siluriformes
<i>Trichomycterus johnsoni</i>	3.2	1.6	SME	Trichomycteridae	Siluriformes
<i>Triportheus pantanensis</i>	2.8	15.8	SME	Characidae	Characiformes
<i>Xyliphius barbatus</i>	3.14	9.2	SMEP	Aspredinidae	Siluriformes
<i>Xyliphius lombarderoi</i>	3.15	9.9	SMEP	Aspredinidae	Siluriformes